THE IMPACT OF GRAZING TIME ALLOWANCE ON THE DRY MATTER INTAKE AND FORAGING BEHAVIOUR OF CATTLE AND DONKEYS MANAGED UNDER TRADITIONAL AFRICAN GRAZING SYSTEMS

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DECLARATION

This thesis has been composed by myself and has not been accepted in any previous application for a degree. The work, of which this is a record, has been done by myself and all sources of information have been acknowledged by means of references.

DAVID GRAHAM SMITH.

In memory of James Stewart MacFarlane 1929 - 1996

ABSTRACT

Restricted nutrient intake is the largest single factor that limits the productivity of grazing animals. Traditional African grazing systems (TAGS) appear to exasperate this constraint by restricting the amount of time available to feed. This project set out to investigate the effect of TAGS on the forage intake of free ranging cattle and donkeys in order that recommendations for their improved nutrition and productivity could be formulated and disseminated to resource-poor livestock owners of Africa.

In order to study the effect of TAGS on cattle and donkey productivity under rangeland conditions, several modifications to the available techniques for estimating dry matter intake (DMI) and collection of behavioural data were made and tested. Modifications in techniques for the estimation of DMI using the ratio technique included: 1) a method for the rapid simultaneous dosing of even-chain alkane and chromic oxide external markers that reduced circadian variation of faecal marker output; 2) the identification of acid-detergent lignin as the most reliable internal marker for the estimation of dry matter digestibility (DMD); 3) the development of an *in vitro* DMD technique that provided reliable estimates of *in vivo* DMD in equids; 4) a hand plucking method for obtaining a representative sample of forage ingested by free-range cattle and donkeys.

Three techniques for automating behavioural data collection were also developed and tested. A method for electronic recording of manually observed behavioural data using a hand-held computer was devised and tested. This device was used successfully in Ethiopia and Zimbabwe, and was found to be less laborious and easier to use than traditional paper-based methods. A second technique for the automation of behavioural data collection using telemetry was developed and tested

in Ethiopia. This device did not prove to be a useful method of collecting behavioural data. The third technique tested was a commercially available bite meter available from the Institut National de la Recherche Agronomique (INRA). Modifications were made that improved both the success rate of data collection and ease of fitting of the device. With practice the INRA device proved to be useful as a method of collecting behavioural data.

An experiment with penned-animals using 4 cattle, 4 donkeys and 4 ponies was carried out in the Scotland. These animal were given eight hours access to either alfalfa, haylage or straw, between 9:00 h and 17:00 h. The DMI, DMD, mean retention time (MRT) and faecal output of the animals were measured over a seven-day period. Behavioural measurements were made over the subsequent seven-day period. Time budgets and circadian behaviour patterns were calculated from 72 hours of observations. In cattle, restricted feed access only resulted in reduced DMI when straw was fed. However, in ponies and donkeys restricted feed access reduced DMI in all three diets fed. Cattle, ponies and donkeys all spent significantly ($P<0.001$) less time eating when fed alfalfa than when fed haylage or straw. A significant relationship ($r^2 = 0.76$, $P< 0.001$) between bite size and bite rate was measured. Bite size and the number of chews per unit mass ingested appear to be closely related to the physical nature and fibre content of the feed offered in both cattle and equids. The effect of restricting access to feed was more severe for equids than for cattle because rates of intake were slower and, because they needed to complete comminution before swallowing.

In Alemaya, Ethiopia, a study of cattle on rangeland was carried out during both the wet and dry seasons using *in vitro* DMD and an external marker to estimate DMI.

Three groups of 4 cattle were provided with either 7-hour grazing access, 7-hour grazing access and given a hay supplement during kraaling, or 11-hour grazing access. Cattle with 7-hour access to grazing achieved the same DMI as cattle with 11-hour access or with 7-hour access plus hay supplement. There was no apparent advantage to extending grazing period or to providing a hay supplement. Cattle given 11-hour access utilised the additional time to graze, spending significantly ($P< 0.05$) longer grazing than those with either 7-hour access or 7-hour access + hay supplement. Cattle with 11- hour access to grazing spent longer eating, but decreased their rate of intake by taking fewer bites per minute. Under the conditions at Alemaya, increasing the amount of time available for grazing or providing supplementary feed did not result in improved DMI.

At Matopos, Zimbabwe, a rangeland study of 12 cattle and 12 donkeys was carried out during both the wet and dry seasons. Each species group (cattle and donkeys) was divided into three groups of four and each group was given was given either 8, 11 or 23 hour grazing access. Cattle with 11-hour grazing access achieved DMI similar to those of cattle with 24-hour access. The DMI of cattle with 8-hour access to grazing was only significantly ($P< 0.01$) less from the 11-hour access group during the wet season. Restricting time of access to grazing had a significant effect ($P< 0.001$) on the DMI of donkeys with both 11-hour and 7-hour access to grazing during the wet and dry seasons. Increasing the time available for eating from 8 to 11 hours had no significant effect on DMI of donkeys.

In Zimbabwe, cattle compensated for restricted feeding time (RFT), firstly, by increasing bite rate, then by increasing eating time per hour (ETPH). Increased bite rate was achieved at the expense of diet quality in cattle with 8-hour access to

grazing during the dry season. The donkeys with free access to grazing spent significantly ($P<0.001$) longer grazing (16 hours per day) than cattle (10 hours). Donkeys with 24-hour access had similar ETPH to that of the other two groups (8-h and 11-h groups) during the common grazing hours. Treatment groups with 8-hour and 11-hour available eating time spent 95% of the available time grazing. Donkeys only increased bite rate to compensate for restricted eating time when grazing access was restricted to 8-hours.

The present study has investigated some of the issues surrounding the management of rangeland resources for the cattle and donkeys of livestock owners in Africa. Restricting the grazing time of cattle to only eight hours per day had no effect on DMI in both Ethiopia and Zimbabwe. Cattle compensate for RFT by increasing ETPH and by increasing bite rate. Traditional grazing management in African communal systems therefore does not appear to significantly limit nutrient intake by cattle. However, the effect of RFT when forage was in short supply was not examined, and further research is required to determine DMI under these conditions.

The effect of TAGS on the nutrient intake by donkeys is much greater than in cattle; restricting the time available for eating limits DMI and reduces the quality of ingested forage. Donkeys must therefore be managed separately from cattle; this is particularly important when they are used for work. Donkeys are much less able to compensate for loss of eating time due to work than cattle, because they need to spend much longer eating.

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ABBREVIATION LIST

ADC	Analogue to digital converter
ADF	Acid detergent fibre
ADL	Acid detergent lignin
AHP	Alkali hydrogen peroxide
AIA	Acid insoluble ash
ALCMF	Alkane labelled chromium mordanted fibre
ALK	Alkane
ANOVA	Analogue to digital converter
ARC	Agricultural Research Council
BCS	Behavioural compensation strategy
BO	Behavioural observations
BR	Bite rate
BS	Bite size
C_{31}	Monatriacontane
C_{32}	Dotriacontane
C_{33}	Tritriacontane
C_{35}	Pentatriacontane
C_{36}	Hexatriacontane
CC	Carrying capacity
CI-ADF	Cellulase indigestible acid detergent fibre
CP	Crude protein
Cr_2O_3	Chromic III oxide
CRD	Controlled release device
CTVM	Centre for Tropical Veterinary Medicine
DM	Dry matter
DMA	Double marker
DMD	Dry matter digestibility
DMI	Dry matter intake
EM-IV	External marker - *In vitro*
EP1	Ethiopian experimental period 1
EP2	Ethiopian experimental period 2
ETPH	Eating time per hour
FO	Faecal output
FT	Feeding time
FW	Fresh weight
GC	Gas chromatography
GE	Gross energy
HP	Hand plucked
IERM	Institute of Ecology and Resource Management
ILCA	International Livestock Centre for Africa
INRA	Institut National de la Recherche Agronomique
IPRED	INRA Portable Electronic Recording Device
IV-ADF	*In vitro* acid detergent fibre
IV-DMD	*In vitro* dry matter digestibility
IV-NDF	*In vitro* neutral detergent fibre

Abbreviations (cont...)

IWL	Insensible weight loss
KB	Kilobyte
KPL	Potassium permanganate lignin
LCD	Liquid crystal display
LWG	Live weight gain
LWT	Live weight
$M^{0.75}$	Metabolic live weight
MAFF	Ministry of Agriculture Food and Fisheries
MB	Megabyte
ME	Metabolisable energy
MLURI	Macaulay Land use Research Institute
MRT	Mean retention time
MSE5	Microsoft excel version 5
MSW6	Microsoft word version 6
N	Nitrogen
NDF	Neutral detergent fibre
NRC	National Research Council
OF	Oesophageal fistula
OM	Organic matter
PC	Personal Computer
PIC	Potentially insoluble cellulose
PO	Psion organiser
PP	Pre-Pepsin
PP+N	Pre-Pepsin plus added nitrogen
QI	Quality index
RCOFV	Remote controlled oesophageal fistula valve
RFT	Restricted feeding time
RI-NDF	Rumen indigestible neutral detergent fibre
TAGS	Traditional African grazing systems
TT	Tilley and Terry
VDU	Visual display unit
VFI	Voluntary food intake
ZP1	Zimbabwean experimental period 1
ZP2	Zimbabwean experimental period 2

CHAPTER 1

INTRODUCTION

1.1: Sustainable development of traditional grazing management systems

Throughout Africa livestock productivity of traditional grazing systems in terms of milk and meat off-take is poorer than that of commercial systems. In Botswana, for example, the productivity of ranching systems is more than twice that of traditional systems (Rennie *et al.*, 1977; de Ridder & Wagenaar, 1986). The development of low-input, sustainable methods of improving productivity of traditional livestock systems could result in the improvement in living standards of the cattle-keeping people of Africa.

The role of livestock in both pastoral and sedentary traditional African societies is complex (Bayer and Waters-Bayer, 1998; Twerda, Fielding and Field, 1997). As well as providing food, animals are used for work, and the manure they produce is a valuable fertilizer (Bayer and Waters-Bayer, 1991). Animals also represent a means of accumulating wealth and are often the currency in which social obligations are fulfilled (Jahnke, 1982). Analysis of productivity simply in terms of meat and milk production may not be entirely appropriate for traditional livestock-keeping communities.

Both pastoralists and sedentary livestock-keeping societies throughout Africa are undergoing a process of spontaneous change (Gränberg and Parkinson, 1988; Lusigi 1986; Jahnke, 1982; Spencer, 1977; ILCA, 1984). There is a desire within these communities to improve their standard of living and an increasing recognition that traditional practices cannot provide the security they once did (Lusigi, 1986). The

increasingly common practice of selling animals to local abattoirs to earn cash represents a transition from subsistence to semi-commercial scale production (Jahnke, 1982). As this trend continues, livestock farmers are becoming more production-orientated, and the requirement for low cost, sustainable methods of improving productivity is increasing.

1.2: Traditional African grazing systems (TAGS)

Night-kraaling, in order to protect livestock from predators and theft or to protect crops from damage by animals, is a common management practice throughout Africa (Bayer and Waters-Bayer, 1998). Typically the animals are herded to *grazing* in the early morning and then returned to the kraal during the late afternoon. Control of grazing animals is generally supervised by herd-boys (Bayer and Otchere, 1985) or, in the case of goats and sheep, by tethering (Romney *et al.,* 1996). Management systems employed for donkeys have not been widely described, but in northern Kenya donkeys are frequently herded together with cattle (Twerda, *et al.,* 1997; Rutagwenda, *et al.,* 1990). Donkeys may also be left unsupervised, although often their movement is restricted with hobbles (Personal Observation; Botswana and Zimbabwe). As donkeys are used mainly for work (Wilson, 1990), they are often kept near to the homestead throughout the day, an area where feed resources are depleted.

The time that animals are taken to *grazing* depends on the farming system and the season of the year. In strictly pastoral communities, where there are few other demands for labour, animals are generally released from the kraal soon after daybreak (Smith, 1961). In mixed systems of crop and animal production, where there are frequently labour priorities above those of herding livestock, animals may not be taken to *grazing* until late in the morning (Bayer and Otchere, 1985). The Fulani

pastoralists of Nigeria avoid grazing their cattle early in the morning during the wet season, in order to reduce animal exposure to helminth larvae (Bayer and Waters-Bayer, 1998). The amount of time animals spend grazing is seldom more than 10 hours and is frequently less than 7 hours (Perrier, 1986).

1.3: The effect of night-kraaling on animal productivity

Restricted nutrient intake is probably the largest single factor which limits the productivity of grazing animals (Hodgson, 1982b) and night-kraaling may further limit nutrient intake by restricting foraging time. Furthermore, although the quality of the available forage is not affected by night-kraaling, there is limited evidence to suggest that animals which were closer to satiety selected a better quality diet than those that were more hungry (Hatfield *et al.,* 1990).

The specific effects that night-kraaling has on livestock productivity have not been widely investigated. Smith (1961) showed that severely restrictive grazing practices (7 hours per day) were only detrimental to live-weight gain of cattle in Zambia when the quality or availability of the herbage was low. The animals compensated for the lack of eating time by spending more time per hour grazing. However, in the Ethiopian highlands Kurtu (1985), estimated that dairy cattle given 7 hours access per day to grazing consumed less than half the dry matter of dairy cattle given free access, and had a significantly lower milk yield.

On improved pastures in Mozambique, Muir, Jordao and Massaete (1995) found that the daily weight gains of goats tethered for 6 hours per day were only 44% that of animals which had 24-hour access to *grazing.* However, Romney *et al.* (1996) working in Tanzania found little difference between the dry matter intake (DMI) of goats tethered at *grazing* for 4 hours, 8 hours or given 8 hours free access to grazing.

Goats with less grazing time compensated for the loss by increasing the eating time per hour (ETPH).

The effect of night-kraaling on donkey productivity has not been investigated. A small-scale study by Blakeway (1994) in Scotland showed that donkeys with free-access to temperate pasture spent a total of ~12 hours per day grazing, and would graze during darkness. This finding was similar to that obtained with free-ranging horses which spent significantly more time grazing than did free-ranging cattle on the same pasture (Arnold, 1984a). Keiper and Keenan (1980) observed free-range horses grazing throughout the hours of darkness, whilst Mayes and Duncan (1986) estimated that up to 55% of the total grazing time of free-range horses occurred at night. In contrast, night-grazing contributes little to the forage intake of cattle (Krysl and Hess, 1993), except under hot and humid climatic conditions (Dulphy, Remond and Theriez, 1980). If donkeys have a similar circadian distribution of grazing to that of horses it is likely that the effect of night kraaling on productivity would be more severe than in ruminants.

1.4: The effect of night-kraaling on foraging behaviour

Gathering forage is a time-consuming activity for all herbivores, representing up to 80% of the daylight time budget (Arnold and Dudzinski, 1978). As well as foraging, other activities during the day, such as ruminating (in the case of ruminants), drinking and resting occupy several hours in each 24-hour period. In arid and semi-arid areas drinking, or at least trekking to a water supply, can occupy up to 2 hours per day, although animals may have the opportunity to graze along the trekking route (Dicko-Tour, 1980; El-Aich, El-Asraoui and Rittenhouse, 1991). Restricting grazing time by night-kraaling places strict constraints on the amount of time an animal can spend

foraging, which may not be readily compensated for by the reduction of time spent in other activities.

In addition to limiting the amount of time that an animal has to eat, restriction of grazing time also radically alters the natural circadian pattern of grazing activity (Bayer and Waters-Bayer, 1998). Foraging activity in animals given free-access to grazing tends to peak during the hours just after sunrise and during the hours just before sunset (Arnold and Dudzinski, 1978; Hodgson, 1990). Under traditional management practices animals frequently miss the opportunity to graze during these periods and are forced to graze during periods of the day which, under natural conditions, they would use for thermo-regulatory activities such as shade-seeking or drinking (Kabuga, Gari-Kwaku and Annor, 1992).

The overall effect of night-kraaling on feeding behaviour is to limit foraging time and to distort natural circadian distribution. The ramifications of these effects on productivity and DMI have not been investigated in detail. Whilst some workers have demonstrated that ruminants are able to compensate for restricted foraging time (Smith 1961; Romney *et al.*, 1996), the mechanism and limits of these strategies have not been investigated.

1.5: Research methodology

Under temperate grazing conditions the methods that are employed to measure DMI and feeding behaviour of free-range herbivores are less precise than those used with penned animals, because there is incomplete control over experimental conditions (Greenhalgh, 1982). Under rangeland conditions, precision is further compromised by the greater diversity of forage-plants, the larger areas over which animals search for food and the practical difficulty of working under arduous conditions. The

measurements made during rangeland studies can, therefore, only be considered as estimates, frequently with no 'Gold standard' against which results can be validated. In developing countries, the degree of difficulty in measuring nutritional parameters for herbivores under rangeland condition is greater. Frequently, basic laboratory facilities such as mains electricity are not dependable or entirely absent and there is limited availability of basic spare parts and reagents. Methodologies and protocols employed must take account of these circumstances, and studies must be planned accordingly.

Lack of precision in methodology should not detract from the importance of rangeland research. Around 44% (~275 million) of tropical cattle are kept under rangeland systems, 90 million of which are managed by traditional pastoral methods (Hill, 1990). Detailed study of the foraging strategies of free-ranging herbivores will contribute much to the understanding of how to manage a delicate ecosystem that is a vital communal-resource. Implementation of improved management strategies could have an enormous impact on the sustainable output of milk, meat and work from traditional systems, resulting in a substantial improvement in the livelihood of poor people in developing countries.

1.6: Research Objectives

Detailed study of both the DMI and feeding behaviour of animals is the key to understanding the strategies that animals adopt when confronted with limited time in which to feed. However, the available methodologies are frequently not well suited for application in developing countries. This thesis presents the findings of 2 research investigations. The first investigation sought to identify and, if necessary, improve available methodologies for investigating the foraging strategies of free-ranging

domesticated herbivores in developing countries. In the second investigation these methodologies were applied to investigate how cattle and donkeys utilise the rangeland feed resource and to exploring possible methods for improving productivity.

In developing methods that could be applied under rangeland conditions, special consideration had to be given to the 2 species of animals that were to be studied. The aim was to develop techniques that could be readily applied to both monogastrics (donkeys) and ruminants (cattle). Furthermore, these techniques needed to have little or no requirement for technical backup. Several major developments in technique are presented in this thesis. In particular, an improved method for recording behavioural data and a modified *in-vitro* technique for the measurement of dry matter digestibility (DMD) in equids are presented. Several modifications to other techniques are also discussed. Application of these techniques allowed efficient implementation of experimental procedures both in the field and in the laboratory.

The initial research work presented in this thesis was carried out in the UK in order to improve the understanding of how cattle and donkeys respond to limited feeding time. To avoid the confounding effects of environment and pasture, this research was carried out using penned animals under experimental conditions where both food availability and quality could be controlled. Findings from this study were used to identify key parameters that could be used to investigate feeding behaviour under tropical rangeland conditions.

The effect of restrictive-grazing practices on animal performance, DMI and foraging behaviour were carried out with cattle in Ethiopia and with cattle and donkeys in Zimbabwe. From this work recommendations have been produced for improving

animals' feed supply that can be readily applied by subsistence-scale farmers in developing countries. In particular, behavioural indicators that help to identify when animals are enduring shortfalls in voluntary food intake (VFI) are presented. If applied correctly, these indicators should allow livestock farmers to identify periods in the year when strategic supplementation would have a net benefit for the individual, both in terms of animal production and labour requirement.

It is recognised that traditional-African grazing systems have developed over many centuries, and that they probably represent a sustainable way of using the fragile, semi-arid rangeland ecosystem. Furthermore, the culture and beliefs of cattle-keeping people of Africa may prevent the wholesale commercialisation of livestock enterprises. Improvements in management practices must, therefore, be modest and fit within the existing systems, without placing additional demands on already stretched human or financial resources.

SECTION 1

METHOD DEVELOPMENT:

CHAPTER 2

DETERMINATION OF DRY MATTER INTAKE BY CATTLE AND DONKEYS FORAGING ON TROPICAL RANGELANDS

2.1: Introduction

The difficulties associated with estimating the DMI of free-ranging animals have already been discussed in Chapter 1, and an ideal method has yet to be developed. One of the aims of the present study was to develop methods for estimating DMI at grazing that could be readily applied in extensive rangeland conditions in developing countries where the amount of technical back-up was minimal. Other factors such as high ambient temperatures and heavy rainfall, which could adversely affect electronic equipment, had to be taken into account when developing a method. Furthermore, the methods are required to be readily applicable to both cattle and donkeys with little or no modification. Available techniques can be broadly grouped into either weighing techniques or ratio techniques and are reviewed below.

2.2: Estimation of dry matter intake at grazing

2.2.1: Weighing techniques

The accurate determination of DMI of animals on rangeland is problematic, since the amount of food eaten cannot be measured directly as it can with penned animals. Weighing methods attempt to quantify DMI by determining the change in available herbage mass, the change in animal live weight or bite weight.

Changes in the herbage mass of sample quadrats before and after grazing can be used to determine the DMI for groups of animals or a single animal, if grazing alone in a

paddock. However, this method can only be used where the grazing is uniform, the area to be grazed is enclosed and the stocking rate is high (Meijs *et al.,* 1982). These conditions are required in order to ensure that the sward is grazed evenly and the animals are, as far as possible, prevented from grazing selectively. It is not an appropriate method for rangeland that is not enclosed and is diverse in terms of both forage quantity and quality.

Other weighing methods for determining DMI at grazing have involved measuring the change in live weight of animals either as they graze, with the aid of telemetric pressure transducers attached to the hooves (Horn, 1981), or at frequent intervals during grazing with sensitive balances (Penning and Hooper, 1985).

The use of the pressure transducer method (Horn, 1981) in rangeland conditions is attractive, especially where telemetry allows data to be transmitted to a remote receiver without any interference with the animal. However, it is doubtful whether pressure transducers would provide reliable data when used in the rough terrain that free-range animals frequently move in, when foraging for food. The equipment is also expensive, and as a consequence, only a limited number of units could be purchased, making it difficult to collect measurements of the DMI of several animals simultaneously.

The measurement of DMI by the pressure transducer method also requires adjustments to be made due to faecal, urinary and insensible weight loss. Whilst, faecal and urinary weight losses can be readily determined with the aid of collection bags and harnesses (Romney *et al.*, 1996), reliable determination of insensible weight losses (IWL) is difficult under free-range conditions. Estimation of IWL

from field measurements of relative-humidity and temperature may not be reliable as animals change their feeding behaviour in response to ambient climate, either in an attempt to control body temperature or to aid water conservation (Payne, 1990).

Although simple in theory, the reliability of determination of DMI by weighing the animal as it eats is limited by the need to apply assumed values to variables that cannot be readily measured, such as IWL. The complexity of the equipment further limits its use in developing countries.

Penning and Hooper's (1985) method of weighing grazing animals at frequent intervals has been successfully used during tropical grazing studies (Romney *et al.*, 1996), particularly where restrictive grazing techniques such as tethering were practised. So far, the method has only been used with small ruminants, such as goats and sheep. At present, portable equipment which can measure the live weight of a 500 kg animal with the degree of precision required (±20 g) is not available (T. Howard, Ruddweigh, Australia; personal communication). The equipment currently available requires a permanent, hard, level surface to function and usually a source of mains power (G. Emerton, Scale Services, Slough, UK; personal communication). Moreover, the equipment requires modification so that the output from the weighing beams can be sampled by a personal computer. The weight of the animal is then calculated from 200 separate measurements taken by the computer (Penning and Hooper, 1985). Whilst it is possible to restrain an animal the size of a sheep for long enough to make these measurements, it is impossible for larger animals, such as cattle or donkeys. Furthermore, the frequent weighing of large animals under

rangeland conditions is not practical as it requires animals to be captured and restrained, which would interfere with natural foraging behaviour.

Another weighing method that has been used extensively on enclosed, temperate pastures involves the determination of bite size. Dry matter intake is estimated from bite size (*Sb*), and the number of bites (*B*) per day, using the following equations (Hodgson, 1986):

$$DMI = B * Sb \qquad \text{(Equation 2.1)}$$

The number of bites is usually determined from the time spent grazing per day (*GT*) and mean bite rate (*Br*), determined by sampling at frequent intervals during the day.

$$\therefore \quad DMI = GT * Br * Sb \qquad \text{(Equation 2.2)}$$

On a given sward, measurement of bite size is the most likely source of variation in the above equations and is, unfortunately, the most difficult to measure (Hodgson, 1986). Time spent grazing and the number of bites can be determined relatively easily by direct observation, with minimal effect on the animal.

Accurate measurements of bite size can only be made using oesophageal-fistulated animals. Traditionally, mean bite size has been determined by recording the number of bites that occurred from the opening of the fistula and the attachment of the sample bag, to the removal of the bag. The dry weight of the fistula extrusa is determined and a mean dry bite size calculated. Typically, samples are taken from an oesophageal-fistulated animal once per day (McManus, 1981), and, therefore, bite-size measurements are derived from a small number of animals over a limited time period.

More frequent sampling from oesophageal fistulas has been made possible by the development of a remote-controlled, oesophageal-fistula valve (RCOFV) (Raats and Clarke, 1992). A radio-controlled switch allows the fistula to be opened from a considerable distance without any physical interference with the animal. Swallowed boli are collected either into bags or from the ground and can be sampled throughout the day, so more detailed descriptions of the diurnal variation in bite size can be obtained. At present, the equipment is only available for goats and sheep, but a device is being developed for cattle (J. G. Raats, University of Fort Hare, South Africa; personal communication).

Problems with the RCOFV include frequent blocking of the fistula and poor recovery rates (Raats *et al.*, 1996). These problems are offset to some degree by stretching the surgically prepared fistula with a series of progressively larger stoppers over a period of weeks (Raats and Clarke, 1992). The final fistula has an elongated oval shape with an area of ~1050mm^2, roughly twice the size of a conventional fistula.

Estimating intake from bite size and number of bites offers several advantages in developing countries. Grazing time and bite rates are easily determined by direct observation. However, bite size is not readily measured, and values obtained with only a few animals must be used. The preparation of oesophageal-fistulates is expensive and time-consuming. There are also serious welfare concerns about the maintenance of such animals in tropical environments, especially where the amount of specialized care they are likely to need is limited. Furthermore, the broad botanical diversity of the diet, including shrubs and trees, of animals foraging on rangeland may mean that determination of DMI from mean bite size is not reliable

Of the weighing techniques available for determining DMI of large animals, none is considered suitable for use in tropical rangeland situations.

2.2.2: Ratio techniques

Ratio techniques for estimating DMI rely on the independent estimation of dry-matter digestibility (DMD) of the diet and the faecal dry matter output (FO) of the animal. Dry matter intake is calculated using the following equation (Hodgson and Rodriguez Capriles, 1971):

$$DMI = \frac{FO}{(1 - DMD)} \qquad \text{(Equation 2.3)}$$

Estimation of faecal output

Faecal output from animals at grazing can be measured directly using faecal collection bags, or indirectly using external markers.

Faecal collection bags provide the most reliable estimates of FO by grazing animals (Galyean, Krysl and Estell, 1986) However it has been suggested that the technique results in depressed live-weight gain (Cordova, Wallace and Pieper, 1978), possibly as a result of stress experienced by harnessed, grazing animals (Hatfield *et al.*, 1993).

In enclosed areas, with little tree or bush cover, the use of faecal collection bags may be possible. However, in a rangeland situation where the foraging area may be very large and bags are likely to get caught on thorn bushes or trees, their use is impractical.

The indirect measurement of FO using external markers is generally used for large animals. Several substances have been suggested as external markers, but

chromium(III) oxide (Cr_2O_3) is most commonly used (Dillon and Stakelum, 1988). More recently, even-chain *n*-alkanes such as dotriacontane (C_{32}) and hexatriacontane (C_{36}) have been used (Dove and Mayes, 1991) and these are considered in detail later. Faecal output can be estimated using the following equation (Hodgson and Rodriguez Capriles, 1971).

$$Fo = \frac{Dem}{Cem} \qquad \text{(Equation 2.4)}$$

Where *Fo* is faecal dry matter output, *Dem* is the amount of external marker dosed per day and *Cem* is the concentration of external marker in the dry faeces. When using this equation the major assumption is that equilibrium has been reached in terms of output and input of the marker.

Good recovery rates of Cr_2O_3 are reported in the literature for both ruminant and equid species. In cattle, Dillon and Stakelum (1988) and Ohajuruka and Palmquist (1991) reported mean recovery values of 93.8 and 99.1%, respectively, for dairy cattle. Piasentier, *et al.*, (1995) reported recovery values for sheep of 94.9%. In horses, Cuddeford and Hughes (1990) and Parkins, Snow and Adams (1982) have reported recovery rates in excess of 94%; similar recovery values were reported in donkeys by Knapka *et al.* (1967).

A major problem with the use of Cr_2O_3 is the circadian variation in the faecal concentration of the marker. In sheep dosed with Cr_2O_3 gelatine capsules twice daily, the circadian variation in faecal concentration of Cr_2O_3 was 29.2% (Furnival, Corbett and Inskip, 1990). In horses dosed once a day with Cr_2O_3-mordanted fibre, Cuddeford and Hughes (1990) showed major circadian variations in faecal Cr_2O_3

concentration. The reliability of FO estimates is greatly affected by this circadian variation, but the effect can be offset by increasing the frequency of faecal sampling (Momont *et al.*, 1994).

The circadian fluctuation in Cr_2O_3 output can be overcome to a large degree by continually delivering a measured dose of marker into the gut (Furnival, Corbett and Inskip, 1990). Intra-ruminal, controlled-release devices (CRD) have been developed for both C_{32} alkane (Dove and Mayes, 1991) and Cr_2O_3 markers for use in both cattle and sheep (Laby, 1981).

Evaluation trials of Cr_2O_3-CRD's using cattle (Pinchak and Hutcheson, 1992; and Hollingsworth *et al.*, 1995) and sheep (Dos Santos and Petit, 1996; Luginbuhl *et al.*, 1994; Buntinx *et al.*, 1992; Furnival, Ellis and Pickering, 1990) have all shown significant differences between measured FO and that estimated using Cr_2O_3. The major source of error is that the release rate specified by the manufacturer is not sufficiently reliable (Brandyberry *et al.*, 1991). Reliability is improved if mean release rates are determined for individual diets in verification trials with penned animals (Pinchak and Hutcheson, 1992).

As there is variability in the release rates of Cr_2O_3 from CRD, caused mainly by the nature of the diet (Doyle *et al.*, 1994), there is no reason to suppose that the C_{32}-CRD are any more reliable than the Cr_2O_3 type. The consensus view on CRD is that they are, at present, insufficiently reliable for use in experimental work (Buntinx *et al.*, 1992; R.W. Mayes, Macaulay Land Use Research Institutre (MLURI), Aberdeen, Scotland; personal communication). A further limitation to the use of CRD in the present study was that they cannot be used in equid species. Methods for the

administration of external markers which can be readily applied to both ruminant and non-ruminant herbivores, and which provide a stable output of the marker throughout the day, need to be developed.

Faecal output can be readily estimated with external markers such as Cr_2O_3 and even-chain alkanes. However, since the concentration of these markers in the faeces is subject to variation throughout the day, which can result in unreliable estimates of FO, recovery rates and circadian variation in faecal concentration of external marker must be established in parallel studies with penned animals. Reliability of FO estimations can also be improved by increasing the frequency of both the marker administration and faecal sampling.

Estimation of dry matter digestibility

The DMD of food selected by a foraging animal can be estimated either by using an internal marker or by using an *in vitro* digestibility technique.

Internal-marker methods

Dry matter digestibility is calculated from the concentration of an internal marker in the DM of the faeces and food, using the following equation (Hodgson and Rodriguez Capriles, 1971):

$$DMD = 1 - \left(\frac{Cimd}{Cimf} \right) \qquad \text{(Equation 2.5)}$$

Where *Cimd* is the concentration of internal marker in the DM of the diet and *Cimf* is the concentration of internal marker in the DM of the faeces.

Internal-marker techniques have the advantage in that they allow DMD for individual animals to be estimated (Dove and Mayes, 1996), and the same method can be used for different types of herbivore, such as ruminants or equids. However, the reliability of internal-marker methods for estimating DMD has often been questioned (Dove and Mayes, 1996; Parker *et al.*, 1990; Langlands, 1975). Poor reliability can be explained by:

i) the empirical nature of the measurement of markers in food and faeces (marker substances measured in faeces are not necessarily chemically identical to those occurring in the food);

ii) the variability in recovery rates of marker substances;

iii) the degree to which food samples reflect the diet the animals have consumed.

Some of these sources of error can be evaluated with parallel *in vivo* studies, but this is not possible for all sources of error such as those that occur during sampling.

Many naturally occurring plant substances have been suggested for use as internal markers. These include acid-insoluble ash, crude-lignin, indigestible fibre and odd-chain *n*-alkanes. Each of these substances offers advantages and disadvantages, but no single method fulfils all the criteria of an ideal marker as suggested by Kotb and Luckey (1972).

Acid-insoluble ash (AIA) is a marker readily determined in feed and faeces. Repeated measurements can be made with a large number of animals and recovery rates are very high (~96%) (van Kuelan and Young, 1977).

In feeding-trials using penned animals, AIA has been used successfully to estimate DMD of diets fed to sheep (Shrivastava and Talapatra, 1962a; Block, Kilmer and Muller, 1981; Hag and Hag, 1983); goats (Hag and Hag, 1983; Trung *et al.*, 1988); cattle (Block, Kilmer and Muller, 1981); and horses (Cuddeford and Hughes, 1990). Acid Insoluble Ash tends to consistently over-estimate DMD (Cuddeford and Hughes, 1990; Penning and Johnson 1983a); some authors have attempted to correct for this bias by applying correction factors derived from regression analysis (Hag and Hag, 1983).

Although AIA has been used successfully to estimate DMD in grazing animals (Shrivastava and Talapatra (1962b), its use in free range studies is problematic because of the risk of contamination of feed and faecal samples with soil-derived AIA. According to a study by Engel, van Schalkwyk and Malan (1975), of sheep foraging natural grasslands in South Africa, poor agreement between AIA-estimated DMD and *in vitro* determination could be explained by soil contaminating the samples. The problem of soil contamination is further exacerbated where animals actively consume soil, as McMeniman, Martin and Dowsett (1990) observed in brood mares grazing natural grasslands in Australia.

Penning and Johnson (1983a) showed that AIA gave poor estimates of DMD for feeds such as lucerne (alfalfa), when the concentrations of the marker in plant tissues were low. On natural South African grasslands, Engel *et al.* (1975) found that at certain times of the year free-range sheep relied heavily on browse species, such as *Felica muricatus*, that have low concentrations of AIA. McMeniman *et al.* (1990)

recommended that the technique should only be used when the concentrations of AIA in dietary samples were more than 25g per kg dry matter (DM).

Although the determination of AIA in both feed and faecal samples is simple, its use in free-range DMD studies is contraindicated because of the risk of soil contamination and the prevalence of browse species in the diet of free-ranging herbivores during certain times of the year.

Lignin has frequently been suggested as an internal marker because no known microbial or mammalian enzyme can degrade it (Fahey and Jung, 1983), and it generally occurs in sufficiently high concentrations in plant tissues to be determined by gravimetric methods (Muntifering, 1982). However, the common analytical procedures of measuring lignin are empirical and succeed only in isolating a crude fraction. This crude-lignin fraction may include components such as cutin and Maillard artefacts, and some true-lignin may be lost in the course of the chemical extraction process (Goering and Van Soest, 1975).

Structural and chemical changes do occur in the crude-lignin fraction during the process of digestion. Fahey, McLaren and Willams (1979) reported apparent-digestibility values of lignin between 17 and 44%. In ruminants, large amounts of lignin can be converted into a soluble lignin-carbohydrate complex in the rumen (Gaillard and Richards, 1975) which is then thought to precipitate in the abomasum (true-stomach) and which subsequently appear as solid material in the faeces (Neilson and Richards, 1978). As a consequence, the substance that is measured as crude-lignin in the faeces is chemically distinct from that measured in the feed. In equids, the site of fermentation (caecum and colon) is posterior to both the stomach

and the major site of carbohydrate absorption (small intestine). The changes that occur in the crude-lignin fragment during digestion are, therefore, likely to be different from that of ruminants, and as a consequence, the reliability of lignin as an internal marker may be different from cattle. There are no published findings on the fate of lignin during digestion in equids.

There are 2 standard gravimetric methods of measuring crude-lignin; these are acid detergent lignin (ADL) (Goering and Van Soest, 1975) and potassium permanganate lignin (KPL) (Van Soest and Wine, 1968). Although KPL gives a closer estimation of true-lignin than does ADL, Van Soest, Robertson and Lewis (1991) considered ADL to be a better internal marker, since faecal recovery is greater than for KPL. ADL offers the further advantage that its determination is less laborious than KPL.

The plant cell wall consists of an intricate matrix of lignin and structural carbohydrates such as cellulose. As the degree of lignification increases, the efficiency of extraction of structural carbohydrates from the matrix during the ADL procedure is lowered because the penetration rate of reagents is reduced (Van Soest and Robertson, 1985). Pre-treatment of samples with alkaline hydrogen peroxide (AHP) disrupts the lignin-carbohydrate complexes and allows ADL reagents to penetrate more rapidly (Cochran, Vanzant and DelCurto, 1988), thus improving carbohydrate extraction (Cameron *et al.,* 1991). Whilst some authors have reported that AHP pre-treatment resulted in a significant improvement in the estimation of DMD over the results obtained with ADL alone (Cochran *et al.*, 1988), others have found no effect (Judkins, Krysl and Barton, 1990).

Crude-lignin estimated by various assays has been successfully used to estimate DMD in penned ruminants. In sheep fed hay-based diets no difference was found between DMD estimated with ADL and that measured *in vivo*, for both AHP pre-treated samples (Momont *et al.,* 1994) and non-AHP pre-treated samples (Sein and Todd, 1988; Thewis, *et al.,* 1989). Sunvold and Cochran (1991) using both ADL and AHP-ADL; and Cochran *et al.* (1988), using AHP-ADL, showed that crude lignin was a reliable marker for estimating DMD in cattle fed hay-based diets. In all these cases, recovery rates of the various crude lignin fractions were close to 100% indicating the absence of both excessive lignin degradation and artefact formation.

However, other scientists have questioned the reliability of crude-lignin as an internal marker. Judkins, Krysl and Barton (1990), using ADL and AHP-ADL, and Muntifering (1982), using KPL and ADL, reported significant differences between estimated DMD based on crude-lignin and that measured *in vivo* in sheep. The same was shown in cattle by Sunvold and Cochran (1991), using ADL and AHP-ADL, Tamminga *et al.* (1989) using ADL and KPL and Cochran *et al.* (1986) using ADL; all found significant differences between crude-lignin estimated DMD and *in vivo* values. In all these cases, recovery rates were between 52 and 122%. The diets used in these experiments were either based on legume hay or had a high level of concentrate supplementation.

In general, crude-lignin appears to give better estimates of DMD for mature, grass-based diets with low levels of supplementation than for those based on young grasses, legumes or concentrates. Lignin appears to be more soluble in conditions where there are high levels of soluble carbohydrate in the rumen.

Galyean, Krysl and Estell (1986) discussed the use of correction factors, based on linear regression, to account for errors in the estimation of DMD. This approach would seem to be of limited benefit in view of the variation in lignin recovery due to different diet composition and the low correlation coefficients (r^2) of such regression equations. Muntifering (1982) corrected DMD, estimated using ADL and KPL, simply by applying recovery values calculated for individual diets, thereby improving the accuracy and reducing the variability of the estimate.

The use of crude-lignin as an internal marker is attractive because of the simplicity of the analytical procedures and its relative abundance in all plant tissues. However, Fahey and Jung (1983) advised the cautious use of crude-lignin markers in view of their unpredictable behaviour in the gut. In practice, crude lignin cannot be used in grazing studies without running parallel control trials with diets similar to those of the grazing animals in order to establish recovery rates. Recovery rates of lignin for these diets must be close to 100% for the use of an internal marker to remain valid. Correction factors, based on recovery rates calculated both for individual diets and individual herbivore species, can be applied to improve the reliability of DMD estimation.

The use of crude lignin for estimating DMD illustrates the problem of using apparently discrete chemical components of plant tissue as indigestible markers. The digestive process is complex and the changes that can occur to both organic and inorganic compounds cannot be readily predicted. The use of these types of marker frequently yields disappointing results because of invalid assumptions made about their behaviour in the gut.

Recently, there have been several attempts to develop markers that are derived from analytical procedures that, to some degree, mimic the digestive process. These markers simply consist of plant fractions that are totally indigestible rather than being discrete chemical components.

The degree to which these techniques mimic the digestive process is variable. The cellulase-indigestible, acid detergent fibre (CI-ADF) technique of Penning and Johnson (1983b) simply incubates food samples with a cellulase to remove the digestible fraction of the plant. Judkins *et al.* (1990) employed *in vitro* digestion techniques based on those of Tilley and Terry (1963), to produce markers such as *in vitro* indigestible, neutral detergent fibre (IV-NDF) and *in vitro* indigestible ADF (IV-ADF). Lippke, Ellis and Jacobs (1986) used *in situ* incubation in the rumen to produce a marker referred to as rumen-indigestible NDF (RI-NDF).

The main disadvantage of these methods is the extended time taken for the incubation of samples in order to prepare markers. The incubation period for CI-ADF (Penning and Johnson, 1983b) is 10 days, for IV-NDF (Judkins *et al.*, 1990) 4 days, and for RI-NDF 6 days (Lippke *et al.,* 1986). In an extreme case of RI-NDF determination, Tamminga *et al.* (1989) incubated samples in the rumen for 30 days.

Penning and Johnson (1983a, b) evaluated CI-ADF as an internal marker and compared the results obtained with 2 other markers, AIA and potentially insoluble cellulose (PIC) and an *in vitro* DMD estimation. It was found that CI-ADF gave a more precise estimate of DMD than did the AIA, PIC and *in vitro* methods. Similar success was reported by Tamminga *et al.* (1989) with CI-ADF-estimated DMD giving the highest correlation with DMD estimated using chromium and cobalt

external markers; CI-ADF has the further advantage that commercially produced enzymes are used in the procedure. The performance of these enzymes is more predictable than the animal-derived enzyme employed in *in vitro* and *in situ* methods.

The various *in vitro* marker methods have been evaluated and compared with other markers by several authors. Krysl *et al.* (1988), Sunvold and Cochran (1991) and Judkins *et al.* (1990) evaluated and compared IV-ADF and IV-NDF markers produced by several different methods. None of these markers estimated DMD any more accurately than crude-lignin; faecal recovery values for both IV-NDF and IV-ADF tended to be lower than for ADL. Nelson *et al.* (1990), using a 96-hour *in vitro* incubation with rumen liquor followed by a 48-hour pepsin incubation, achieved IV-ADF recovery rates of 97% and succeeded in estimating DMD accurately (± 2%) compared to *in vivo* values. Both IV-ADF and IV-NDF have still to be evaluated in equids.

The value of *in vitro*-derived markers (IV-markers) has to be questioned following the work of Judkins *et al.* (1990) who showed standard *in vitro* DMD techniques to be superior to IV- markers. Although IV-markers have the advantage that they allow DMD to be calculated for individual animals, these estimates are likely to be unreliable if recovery rates are low.

Rumen Indigestible NDF use as a marker has been evaluated by Lippke *et al.* (1986); Judkins *et al.* (1990) and Fondevila *et al.* (1995). Lippke *et al.* (1986) obtained variable recovery rates of between 82 and 127% with RI-NDF; DMD was not estimated. The RI-NDF estimated by Judkins *et al.* (1990) for various diets was the least accurate of all markers tested, over-estimating DMD by between 6 and

14%; recovery rates were not stated. Fondevila *et al.* (1995), however, reported good agreement between *in vivo* DMD and that estimated with RI-NDF; recovery rates were close to 100%.

The routine use of *in vitro* markers and RI-NDF for a large number of samples is impractical because of the need to use rumen-fistulated animals (Penning and Johnson, 1983b). Moreover, these laborious methods are no more reliable than crude-lignin markers. Furthermore, the application of these methods to equids is not feasible, as caecally-fistulated horses are not readily available.

A 'perfect' marker for estimating DMD in grazing studies in tropical countries does not exist. The most likely methodologies worth further experimental investigation are ADL and CI-ADF; the analytical techniques for these markers are simple and require no specialised equipment or surgically-adapted animals. However, because the reliability of both these markers is variable there is a requirement to run parallel control studies to establish recovery rates and to test the reliability of the markers under prevailing experimental conditions.

Determination of both ADL and CI-ADF on the same set of samples would allow comparison between DMD estimated by both methods and would involve no additional fieldwork. It may also be possible to carry out these procedures sequentially, by determining the ADL content of the CI-ADF residue. Comparisons of marker-estimated DMD with *in vitro* values would act as a useful cross-check for the reliability of DMD values obtained from animals at grazing. Recovery rates and correction factors can be determined from parallel *in vivo* studies with penned animals.

In vitro methods

In vitro DMD (IV-DMD) is more commonly used than internal markers to estimate DMD of grazing (Hodgson and Rodriguez Capriles, 1971). The 2-stage Tilley and Terry (TT) (1963) method, or modifications of it, are generally used to determine IV-DMD.

Although IV-DMD overcomes many of the inherent inaccuracies of marker methods, DMD estimates are usually derived from a single forage sample and applied to all individuals in the study (Dove and Mayes, 1996). This may be a considerable source of error, particularly where there is a large diversity of plant species within the grassland. Furthermore, IV-DMD values are often applied to animals which are of a different class or species from those used to determine the *in vitro* / *in vivo* calibrations (Dove and Mayes 1996).

A particular problem with the use of IV-DMD in the current project was that the study involved both cattle and donkeys. The standard technique, (Tilley and Terry, 1963), was developed for use in ruminants and satisfactory end point *in vitro* methods based on this method have not been developed for equids.

The development of a TT method for determining the DMD of donkeys' diets should be possible, providing feeds of known DMD are used to calibrate the method. The DMD of donkey diets can be used in Equation 2.3 to estimate DMI.

2.2.3: The use of n-alkane pairs as markers for estimating dry matter intake

Mayes *et al.* (1986) proposed the use of n-alkanes to measure intake. Technically this is a double-marker method, which relies on the use of a naturally occurring plant substance (odd-chain alkanes) to estimate DMD and a dosed substance (even-chain

alkanes) to estimate FO. However, the use of consecutive pairs of alkanes (for example C_{31} and C_{32}, C_{32} and C_{33} or C_{35} and C_{36}), with Equation 2.6, means that in practice, the pair of alkanes are effectively working together as a single intake marker.

$$DMI = \frac{\frac{Fi}{Fj} * Dj}{\left(Hi - \frac{Fi}{Fj} * Hj\right)} \qquad \text{(Equation 2.6)}$$

Where *DMI* is dry matter intake, *Fi* faecal DM concentration of odd-chain alkane, *Fj* faecal DM concentration of even-chain alkane, *Hi* herbage DM concentration of odd-chain alkane, *Hj* herbage DM concentration of even-chain alkane and *Dj* is the daily dose of even-chain alkane.

The use of pairs of alkanes overcomes 2 of the major problems of estimating DMI using indigestible markers. Firstly, alkanes are chemically discrete and appear in the same chemical form in both faecal and plant material (Dove and Mayes, 1996). Secondly, when DMI is calculated using pairs of consecutive alkanes there is no requirement to take recovery rates into account (Dove and Mayes, 1991), because each alkane of the pair is digested to the same extent.

Dosed, even-chain alkanes appear to disperse more readily in the gut and mix more intimately with the gut contents than Cr_2O_3 (Mayes *et al.* 1986; Furnival, Corbett and Inskip, 1990 and Vulich and Hanrahan, 1995), resulting in less circadian variation in faecal marker concentration. Malossini, *et al.* (1996) reported less within-day variation in alkane concentration than Cr_2O_3 in grazing dairy cows dosed twice per day.

The standard method of dosing alkanes is to spray filter paper sheets with a solution of even-chain alkane dissolved in *n*-alkane. The filter paper is dried, then heated to 100 °C for 2 minutes, before being shredded and made into pellets (Mayes *et al.*, 1986). Other methods have also been successfully used. For example, Marais *et al.* (1996) developed a liquid dosing method, where the alkane was administered using a conventional drenching gun. Milled grass particles were coated with alkane then suspended in xanthan gum. The mixture was then dispensed through a dosing gun, using a volumetric method to measure dose rate. Ohajuruka and Palmquist (1991) dosed gelatine capsules containing pure C_{32} alkane mixed with a lecithin carrier.

Alkanes can be melted onto practically any absorptive material (C. S. Lamb, MLURI, Aberdeen, Scotland; personal communication). The opportunity, therefore, exists to dose both Cr_2O_3 and an even-chain alkane simultaneously by labelling Cr_2O_3-mordanted fibre with the alkane. This method would allow FO obtained in the field to be verified using 2 methods.

Increasing both the frequency of even-chain alkane dosing and faecal sampling reduces circadian variation in the faecal concentration of the marker, resulting in more reliable estimates of DMI (Vulich and Hanrahan, 1995). Alkane pairs have been thoroughly evaluated as intake markers in trials with penned animals. Mayes *et al.* (1986), Vulich, O'Riordan and Hanrahan (1991) and Piasentier *et al.* (1995) showed no significant difference between measured *in vivo* DMI and that estimated with alkane pairs in sheep. Dillon and Stakelum (1988) reported similarly reliable results for dairy cattle.

In grazing studies, several comparisons have been made between the alkane method and other indirect methods. Dove, Foot and Freer (1989) obtained estimates of DMI that were close to those estimated with the Cr_2O_3 / *in vitro* method. The small differences between methods were explained by the effect of levels of intake on digestibility. Malossini *et al.* (1996) reported no significant differences between DMI estimated with alkanes and those obtained using the Cr_2O_3 / *in vitro* method.

Tropical forages tend to have lower levels of C_{31} and C_{33} alkanes, and have proportionately higher levels of C_{27} and C_{29} alkanes than temperate forages. This poses a problem for the use of alkanes in estimating DMI, as levels of the odd-chain alkane, in the alkane pair, may not be sufficiently high to provide reliable DMI estimates (Laredo *et al.,* 1991). Where more abundant, shorter-chain alkanes (C_{27} and C_{29}) were used to replace C_{31} or C_{33} in an alkane pair precision of the alkane method was decreased by approximately 8%. Some common tropical forages, such as *Leucaena leucocepala,* contain insufficient quantities of alkane to estimate DMI (Laredo *et al.*, 1991). Similar problems were identified with the use of other legume forages by Casson *et al.* (1990).

Alkanes have been used successfully to estimate DMI by animals grazing tropical grasslands. Reeves *et al.* (1996) found close agreement between DMI estimated with a C_{33}/C_{32} alkane pair, direct sward measurement and predictive models based on energy requirements in cattle grazing kikuyu grass *(Pennisetum clandestinum)* swards. Romney *et al.* (1996) used a C_{33}/C_{32} alkane pair to estimate DMI in tethered goats on *Bracharia*-dominated swards in Tanzania, and obtained close agreement with data derived using Penning and Hooper's (1985) animal weighing method.

Reasonable estimates of DMI by animals grazing tropical swards can be obtained with alkanes, but care must be taken to account for the alkane content of each forage species that contributes to the herbivore's diet (Casson *et al.*, 1990). This may especially be the case where animals ingest a lot of browse species. Browse species such as *Acacia karroo, Ehretia rigida* and *Leucaena leucocepala,* as well as major grass species such as *Seteria sphacelata,* have very low concentration of C_{31} and C_{33} alkanes (Laredo *et al.*, 1991; de Bruyn and Marais, 1996). The use of a C_{31}/C_{32} or a C_{33}/C_{32} pair in situations where these plant species predominate in the diet can significantly reduce the reliability of the estimation of DMI.

Another difficulty associated with the use of alkanes as markers is the complexity and expense of the analytical technique (Romney *et al.*, 1996). The use of gas chromatography (GC) to determine alkane concentrations is not a widely available analytical procedure. The preparation of a GC standard solution containing a known proportion of every alkane between C_{25}-C_{36} requires the skills of a chemist. As the determination of alkane concentration depends entirely on this standard solution accurate preparation is essential (R. W. Mayes, MLURI, Aberdeen, Scotland; personal communication).

Facilities for analysing alkanes have been successfully established in developing countries such as South Africa (Marais *et al.*, 1996) and Zimbabwe (Z. Madgidzare, Matopos Research Station, Bulawayo, Zimbabwe; personal communication). However, the complexity of analysing *n*-alkanes has resulted in analytical facilities becoming centralised in specialist laboratories; their distant location greatly increasing the amount of time taken to obtain results.

A further constraint to the use of alkanes is the increasing difficulty in obtaining C_{32} or C_{36} alkane for dosing animals (R. W. Mayes, MLURI, Aberdeen, Scotland; personal communication). Although alkane CRD are available from Captec, New Zealand, their reliability for use in experimental work has yet to be established.

2.2.4: Obtaining a representative sample of ingesta

The reliable estimation of DMI by indirect methods depends to a large degree on whether feed samples are representative of what the animal has selected to eat. Obtaining such dietary samples under rangeland conditions is particularly difficult.

Two methods are currently used to obtain representative samples of ingested food: samples of selected plants may be hand-plucked (HP) by trained observers closely following the animals or, extrusa may be obtained from oesophageal-fistulated (OF) animals (Jones, 1981).

The OF method is generally considered superior to hand-plucking, and is the method of choice for gathering forage samples. This is because the sample is truly representative of what an animal has actually ingested, thus eliminating any subjectivity on the part of the sampler (Le Du and Penning, 1982).

Although technically difficult to establish and maintain, fistulated animals have been widely used in tropical African countries such as Nigeria (Njwe *et al.*, 1995), Zimbabwe (Nyamangara and Ndlovu, 1995) and Mali (Schlecht, Sangar and Becker, 1995).

A broad range of other herbivore species has been fitted with OF, including red deer (*Cervus elaphus*) in New Zealand (Semiadi *et al.*, 1993) and alpaca (*Lama pacos*) in

Peru and Bolivia (Reiner and Bryant, 1986). However, the use of OF in equids has been rarely reported. Ralston (1982) carried out the surgical procedure in 7 ponies, only 4 of which were used in experiments. There are no reports of the procedure having been carried out in donkeys.

The reliability of the OF technique for animals foraging within diverse plant communities has recently been questioned (Jones and Lascano, 1992). In this situation, the underlying assumptions that the OF extrusa samples are the same as the feed selected by a non-fistulated animal, may be ill-founded. The principal source of error is that extrusa samples from OF are usually collected only once per day, generally in the morning, after a period of fasting (Coates, Schachenmann and Jones, 1987). As herbivores are likely to pass through several micro-communities of plants throughout the course of the day, samples taken only once per day are unlikely to be representative of the whole diet. Furthermore, animals that have been fasted are unlikely to select the same plants or plant parts as animals that are close to satiety (Jones and Lascano, 1992).

The failure of extrusa samples from OF animals to be representative of ingested material was demonstrated by Coats *et al.* (1987) and Jones and Lascano (1992) using a technique that discriminated between tropical legumes and tropical grasses (Ludlow, Troughton and Jones, 1976). Raats *et al.* (1996) showed that increasing the sampling frequency (using RCOFV), improved the agreement between the grass content of extrusa samples and the observed frequency of grass selection.

Hand plucking is a technique which has generally been considered to be laborious and prone to operator error (Jones, 1981). However, it does have the advantage that

numerous samples can be taken throughout the day without any direct interference with the animal, and samples can be gathered for all animals in the experimental group. Semiadi *et al.* (1993), in an experiment using red deer on enclosed pasture, have shown that hand-plucked samples were almost identical to extrusa samples from OF (the current method of choice), in terms of organic matter digestibility and species composition.

The HP technique is becoming an increasingly popular research method amongst rangeland research workers in developing countries including India (Sharma *et al.*, 1998), Tanzania (Romney *et al.*, 1996) and Cameroon (Njoya, 1997). The technique can be readily adapted for use with all but the most timid herbivore (Maisels, 1988) and has been used with brood mares in Australia by Gallagher and McMeniman (1988).

A major problem with the technique was obtaining a sample that was quantitatively representative of the animal's diet. Various methods have been adopted to try to ensure that this will occur. Gallagher and McMeniman (1988) sampled everything a horse selected to eat for a period of one minute every 15 minutes over the course of the day, whilst Holst, Hall and Nolan (1996) trained observers to pay special attention to the plant part (either stem or petiole) that sheep selected. The general assumption with these methods is that the time spent consuming a plant is proportional to the amount of that plant eaten (Sharma *et al.*, 1998). Even when an attempt is made to quantitatively represent selected species in a diet by mimicking the frequency of selection, there is still a source of error in that the size of each hand-plucked sample will vary.

Determining those individual species that contribute to the diet becomes problematic in closely grazed, compact swards. However, the opportunity for a herbivore to select individual species under these conditions is limited, and thus selectivity is likely to be confined to patch selection or choice of grazing horizon (Illius and Gordon, 1993). Sampling can, therefore, be less rigorous, with sample cuttings being taken from in front of the grazing animal, above the grazing horizon (Malossini *et al.*, 1994).

The use of OF extrusa samples in diverse rangeland situations is likely to lead to errors in the estimation of DMD because of the unrepresentative nature of the sample. Although laborious, the HP technique can provide a representative sample and be readily implemented in developing countries where labour is cheap and the training required is minimal.

2.3: Conclusions

Weighing methods for estimation of DMI are, on the whole, either not appropriate or insufficiently developed for use with large herbivores foraging on tropical rangeland. The best method within this group of techniques is that based on bite size. However, even this method has inherent inaccuracies when used under rangeland conditions because of the difficulty in obtaining a reasonable estimate of mean bite size.

The best method currently available for the estimation of DMI under rangeland conditions is the ratio technique. The main source of error associated with the ratio technique is the accurate estimation of DMD. Whilst, DMD may be estimated by internal markers or *in vitro*, both methods are imperfect and require further

development and testing to find which approach works best under the prevailing rangeland conditions.

There are few problems associated with the use of external markers to estimate FO provided that marker recovery rates are determined by total faecal collection with individually penned animals. Care must also be taken to reduce circadian variation in the faecal concentration of the external maker by increasing both the frequency of marker administration and faecal sampling. Marker recovery rates should be determined using diets similar to those encountered by animals at grazing and preferably using the same animals that are used in any grazing studies. Thus, every grazing study should be supported by a parallel study using penned animals.

The administration of an external marker presents a problem in the current study because the use of both cattle and donkeys in the grazing experiments precludes the use of CRD. A method that can be readily applied to both equine and bovine species, so that animals can be dosed quickly and efficiently once or twice per day, needs to be developed.

The reliability of the marker technique for estimating DMD is limited by the lack of a discrete plant substance that fulfils all the criteria of Kotb and Luckey (1972). The 2 internal-markers that are likely to provide the most reliable estimation of DMD are crude-lignin and CI-ADF. The reliability of these markers has, however, not been conclusively established. These markers should be tested using penned animals fed diets that are diverse in terms of quality and plant species. In particular, the recovery rates of these 2 internal markers and the value of AHP pre-treatment of samples should be ascertained.

The determination of DMD through the use of *in vitro* methods overcomes many of the limitations in using internal markers. However, the laborious nature of the technique limits the extent to which samples can be replicated. Traditionally, the DMD of only one diet sample per treatment was determined by *in vitro* methods, typically obtained from an animal fitted with an OF. The assumption that all animals at grazing select a diet of equal quality in diverse rangeland habitats is likely to be invalid. The DMD values estimated from *in vitro* studies should, therefore, be regarded with caution, and perhaps used in conjunction with other methods of estimating DMD.

End point, *in vitro* DMD methods (e.g. TT) have not been developed for equine species. If *in vitro* methods are to be used in grazing studies that involve both cattle and donkeys, there is a need to develop a method for equids.

Methods used for obtaining dietary samples from animals at grazing have a great influence on the reliability of DMI estimation. Several authors have compared methods such as OF and HP sampling techniques, although the rigour of these comparisons has been limited by the technical difficulty of conducting such comparisons. Traditional OF sampling techniques that involve taking samples once per day cannot fully represent all the ingested components of an animal's diet. Hand plucking techniques are simpler to apply under conditions found in developing countries and, if the samplers are carefully trained, should provide a better method of obtaining representative samples than once-per-day sampling with OF.

The reliability of current ratio methods for estimating DMI of animals foraging upon tropical rangeland is limited by shortcomings in methodologies for estimating FO and DMD. Some of these problems, such as the validation of internal markers, can

be addressed by experiments carried out using penned animals. Others problems, such as establishing the efficacy of alkane pairs as intake markers under tropical conditions, require testing using free-range animals foraging upon tropical rangeland.

From a review of the literature, 3 methodological problems were identified that could be solved by developmental research carried out in the UK. These were i) the absence of a reliable dosing method for administering external marker to estimate FO; ii) unequivocal data on the most appropriate choice of internal marker to estimate DMD; iii) the lack of an *in vitro* method for estimating the DMD for equines. The following chapter presents the results of 3 studies carried out in the UK to address the research issues identified.

CHAPTER 3:

VALIDATION AND DEVELOPMENT OF EXTERNAL AND INTERNAL MARKER TECHNIQUES

3.1: External marker preparation, bolus manufacture and dosing techniques

3.1.1: Background

The external marker method of estimating FO at grazing is a well-proven and reliable technique. The main source of error with this technique is the circadian variation that occurs in the faecal output of external markers. This effect can be reduced by increasing the frequency of dosing or by the use of CRD but these cannot be used in non-ruminant herbivores such as the donkey. A technique was required that could be applied equally to equids and ruminants and that allowed the rapid and efficient dosing of marker to animals once or twice per day.

Another possible way of reducing circadian variation in external marker output was to increase the fibre length of the carrier fibre to which the external marker was attached. The theory behind this was that an increase in fibre length would delay the markers passage through the gut and increase the degree of mixing with the gut contents thereby reducing pulsed output of external marker (Stevens and Hume, 1995).

In addition to the requirement for a dosing technique, it was considered desirable to develop a method that would allow the simultaneous dosing of Cr_2O_3 and C_{36}, so that FO could be measured simultaneously with 2 markers.

3.1.2: External marker preparation

Cr_2O_3 and C_{36} markers were to be dosed simultaneously using a carrier fibre onto which the Cr_2O_3 would be mordanted and the C_{36} would be adsorbed.

The preparation of a large quantity (12 kg) of chromium-mordanted-fibre was achieved using a modified version of the method described by Uden, Colucci and Van Soest (1980). Crude NDF was prepared from hay which had been milled through a 4 mm-screen. The large screen size was chosen to produce a fibre with a mean particle size greater than 2 mm, so that retention time in the rumen would be extended and a more intimate mixing with the gut contents achieved. The hay was then boiled with a commercial clothes-washing detergent (Persil, Lever Brothers) for 1 hour.

The resultant fibre was then placed in large nylon bags, which were fastened and rinsed on a cool wash cycle in a domestic washing machine (Hoover Model 1300). After the rinse cycle had been completed, the bags were removed from the machine and rinsed in acetone until the liquid squeezed from each bag was colourless. Further liquid was expelled from the fibre by spinning in a domestic spin-drier (Hotpoint Model 80) at 800 rpm. The bags were then dried in a domestic tumble-drier (Zanussi Model 35C) set on 'Low Heat' for 20 minutes. To prevent excessive balling of the fibre, the bags were removed from the tumble-drier before being completely dry. The fibre was then placed on large trays and dried in a forced-draught oven at 60°C for 24 hours.

Batches of approximately 2 kg of chromium-mordanted-fibre were prepared by placing a known amount of fibre in a large domestic boiler (Belco 10). Sodium

dichromate granules were then added to the fibre, at a rate of 0.4 x the weight of dry fibre. Warm water was added to the boiler and the mixture was heated to boiling, stirred, and the boiler then sealed with aluminium foil. After placing the lid on the boiler, the mixture was allowed to simmer on a low heat for 24 hours, then placed in nylon bags, which were tied and rinsed in the washing machine for 10 minutes. The fibre was then placed in a large bucket and ascorbic acid was added at a rate of 0.5x the weight of the dry fibre. Sufficient cold water was added to the fibre to suspend all the particles, and the solution was allow to stand for an hour before being rinsed, spun and dried as described above.

When 12 kg of chromium-mordanted-fibre had been prepared, C_{36} alkane was adsorbed on to the fibre surface, using a method modified from Mayes, Lamb and Colgrove (1986). A solution of pure alkane (C_{36}) in n-heptane (97 g per litre) was prepared and sprayed, over a period of 10 minutes with the aid of a hand-spray gun, on to 3 kg batches of mordanted-fibre while it was being spun in a small rotary cement mixer. The fibre was placed on trays and dried at room temperature in a well-ventilated place. The batches of fibre were then placed in an oven at 100°C for 10-20 minutes to melt the alkane on to the fibre.

Four 3-kg batches of alkane-labelled, chromium-mordanted-fibre (ALCMF) were placed in a large plastic bag and mixed thoroughly. Five 10-g samples of ALCMF were analysed for chromium and alkane concentration. These data were used to calculate the dosing rate of the finished fibre.

3.1.3: Bolus preparation

The ALCMF was given to the animals in the form of a 5 g bolus. Boli were formed using modified 50 ml plastic centrifuge tubes. The conical bases of the tubes were perforated with a 10 mm hole and a tight fitting rubber bung (size 22) placed in the neck of the tube and pushed down toward the conical tip. A 25 mm filter disc was then placed in the tube and pushed down to rest on the rubber bung. With the aid of a wide-necked funnel 5 g ALCMF was tipped into the modified centrifuge tube. The fibre was then loosely compressed and 5 ml of warm five per cent gelatine solution added. Another 25 mm filter disc was placed on the top of the fibre, and the lid of the centrifuge tube, which had been previously perforated with a 5 mm hole, screwed into place. The contents of the tube were then compressed into a moderately compact bolus with the aid of a metal rod inserted though the hole in the conical end of the tube. Once made the boli were placed in a refrigerator at 4°C until required.

Excessive compression of the bolus was avoided because it could result in the bursting of the paper filter disc, and the loss of some fibre from the tube. Furthermore, the boli were intended to collapse when chewed, following dosing. Highly compressed, hard boli were easier for the animal to reject than soft ones which collapsed easily under pressure within the mouth.

3.1.4: Dosing technique

Boli were given to the animals with the aid of a specially enlarged Foulk's balling gun. Animals were restrained with the aid of a neck yoke. In the case of cattle the bolus was placed over the tongue into the back of the throat. In donkeys the throat was too narrow to allow effective dosing in this way. When placed at the back of the tongue the donkeys were frequently able to recover the boli and eject them from their

mouths. To overcome this problem, a drop of peppermint oil was added to each bolus to make it more palatable; the soft texture and palatability of the bolus then made rejection unlikely. Animals were released from the neck yoke and observed closely for 2-3 minutes to confirm that the boli had been swallowed.

3.2: Evaluation of ADL and CI-ADF as internal markers for estimating DMD

3.2.1: Background

In order to identify an internal marker which would provided a reliable estimate of DMD, several were tested using feed and faecal samples from an *in vivo* DMD trial, measured using 4 cattle, 4 donkeys and 4 ponies fed alfalfa, haylage or straw.

3.2.2: Materials and method

The markers tested were cellulase-indigestible, acid detergent fibre (CI-ADF), acid detergent lignin (ADL), alkaline hydrogen peroxide pre-treated CI-ADF (AHP-CI-ADF) and alkaline hydrogen peroxide pre-treated ADL (AHP-ADL). *In vivo* DMD, feed and faecal samples were obtained from an experiment described in Chapter 6.

Feed and faecal samples were analysed for CI-ADF using a method adapted from Penning and Johnson (1983b), and ADL using the method described by Van Soest and Robertson (1985). ADL and CI-ADF analysis were also made on a duplicate set of samples that had been pre-treated by incubating at 22°C for 24 hours in one per cent alkaline hydrogen peroxide (pH 11.5) (AHP), according to the method of Sunvold and Cochran (1991).

The CI-ADF method was modified, as follows, in order to reduce losses in the transfer of material from the incubation vessel to the filter vessel. After extraction

with acid-detergent solution, the ADF was retained in sintered crucibles, which were placed in a plastic box. Approximately 30 ml of cellulase solution (pH 4.6) was added to each crucible The box was then placed inside a large, re-sealable plastic bag and incubated for 10 days at 40°C. The box was removed from the incubator each day, the contents of each crucible stirred with a glass rod and the cellulase solution topped-up. At the end of the incubation period, the solution remaining in the crucibles was filtered under vacuum, and the crucible contents rinsed several times with hot water (80°C). With this method it was found that, compared with the non-adapted method, the variation between duplicate samples was much reduced.

The AHP treatment was also modified in the same manner as established for the CI-ADF treatment. After ADF extraction, sintered crucibles were placed in a plastic box, and AHP solution was added to each crucible. As AHP solution slowly drained through the sinter, each crucible was refilled with solution to within 1 cm of the rim. The contents of each crucible were stirred at least 3 times during the 24-hour incubation period.

After AHP treatment the samples were thoroughly washed with hot water (80°C). In the case of the CI-ADF analysis, the samples were given a final rinse with five per cent citric acid solution to neutralise any remaining alkali residues. Samples were then soaked for 1 hour in the same buffer solution as was used to prepare the CI-ADF cellulase solution to stabilise the pH of the fibre to 4.6. The remaining buffer solution in the crucibles was then filtered under vacuum and the normal CI-ADF procedure followed. Where samples were to be analysed for ADL, the crucibles

were dried at 100°C overnight after the hot-water wash before being treated with 72 per cent (12 M) H_2SO_4 for 3 hours at room temperature.

Dry matter digestibility estimated with each internal marker was calculated using Equation 2.5 (page 18). These data were compared with *in vivo* DMD for cattle, donkeys and ponies for each feed. Faecal recovery of each marker was calculated using FO and DMI data obtained from the experiment reported in Chapter 6.

3.2.3: Results

The accuracy of the internal markers for estimating DMD was highly variable (Table 3.1). Acid detergent lignin gave the closest values to *in vivo* DMD values (mean residual error ±2%) followed by AHP-CI-ADF (mean residual error ±5%), AHP-ADL (mean residual error ±6%), and CI-ADF (mean residual error ±9%) The difference between *in vivo* dry matter digestibility and that estimated using the various internal markers tended to increase as the indigestible portion of the diet increased (Figure 3.1).

Table 3.1: Comparison of CI-ADF, AHP-CI-ADF, AHP-ADL and ADL estimated dry matter digestibility (proportion in DM) with mean *in vivo* dry matter digestibility of haylage, alfalfa and barley straw fed to donkeys, cattle and ponies (± s.e.).

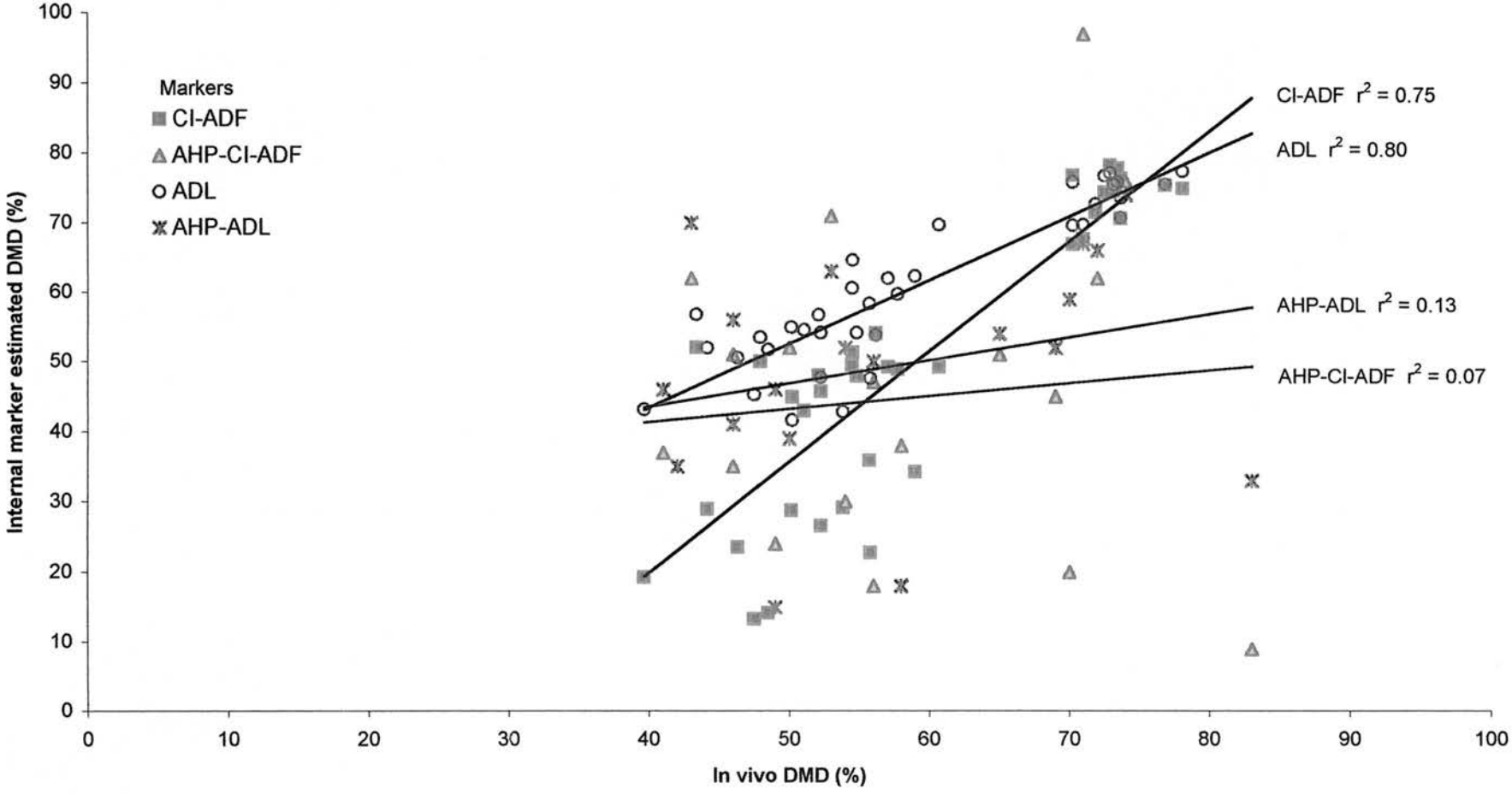
	Mean dry matter digestibility coefficients			
	All animals (n = 36)	Donkeys (n = 12)	Cattle (n = 12)	Ponies (n = 12)
In vivo	0.59 (0.043)	0.60 (0.059)	0.60 (0.051)	0.57 (0.083)
CI-ADF	0.50 (0.074)	0.50 (0.132)	0.50 (0.094)	0.49 (0.122)
AHP-CI-ADF	0.54 (0.085)	0.53 (0.084)	0.65 (0.145)	0.44 (0.108)
ADL	0.61 (0.046)	0.59 (0.073)	0.64 (0.047)	0.59 (0.083)
AHP-ADL	0.53 (0.03)	0.53 (0.071)	0.61 (0.099)	0.44 (0.077)

Recovery rates of the markers were highly variable (Table 3.2); those for ADL were closest to 100% in all 3 species with an overall recovery rate of 104.9%. The overall recovery rates for the other 3 markers were less than 90%.

Table 3.2: Mean recovery rates (%) of CI-ADF, AHP-CI-ADF, AHP-ADL and ADL internal markers in cattle, donkeys and ponies (± s.e.) fed haylage, alfalfa or barley straw.

	Mean recovery rates			
	All animals (n = 36)	Donkeys (n =12)	Cattle (n=12)	Ponies (n =12)
CI-ADF	85.9 (3.03)	91.2 (7.37)	82.0 (3.16)	84.5 (4.21)
AHP-CI-ADF	78.1 (7.75)	85.5 (12.78)	71.2 (9.33)	77.6 (18.14)
ADL	104.9 (2.16)	102.5 (4.09)	108.5 (3.22)	103.7 (3.56)
AHP-ADL	80.9 (4.51)	84.1 (6.30)	84.4 (2.51)	71.3 (11.36)

Figure 3.1: Relationship between in vivo DMD and DMD estimated with cellulase indigestible acid detergent fibre (CI-ADF), acid detergent lignin (ADL), alkali peroxide pre-treated CI-ADF (AHP-CI-ADF) and alkali-peroxide pre-treated ADL (AHP-ADL) in donkeys, cattle and ponies fed haylage, alfalfa or barley straw.



3.2.4: Discussion

Acid detergent lignin proved to be the most reliable marker of the 4 tested because it had the lowest residual error (+2%) and provided accurate estimates of DMD for feeds with a wide range of indigestible fibre content (ADF 288–529 g/kg DM). In addition, the ADL technique was the least complex and most rapid of the 4 tested, and could be incorporated most easily into a standard analytical routine.

The recovery rate of ADL was closer to 100% in donkeys and ponies than it was in cattle. In cattle DMD was overestimated by 4%. The difference in recovery rates of ADL between cattle and equids may be explained by formation of soluble complexes between lignin and carbohydrate during anaerobic fermentation. The complexes then condense to form "artefact" ADL which appears in the faeces (Fahey and Jung, 1983). In the equid gut, most soluble carbohydrate is digested before being exposed to anaerobic fermentation thereby inhibiting the formation of "artefact" ADL and so improving recovery rates. Differences in recovery rates of ADL between cattle and equids mean that different correction factors must be applied when this marker is used to estimate DMD at grazing in these species.

Agreement between DMD estimated using markers and that measured *in vivo* increased with digestibility (Figure 3.1), probably as a result of a more rapid penetration of the lignin-cellulose matrix by reagents. The reliability of CI-ADF was less than ADL when DMD was low, probably as a result of the exhaustion of the cellulase. Although Penning and Johnson (1983b) did not show the same relationship between feed quality and CI-ADF reliability, these workers used feeds with a range of *in vivo* DMD between 0.57 and 0.84, whilst in the current experiment, *in vivo* DMD ranged from 0.39 to 0.78. Cochran *et al.* (1986) also

reported that ADL gave better estimates of DMD than did CI-ADF, confirming the findings of the current study that ADL gives the best estimates of DMD over a wide range of feed types.

Pre-treatment of samples with AHP did not improve the reliability of the estimation of DMD using ADL or CI-ADF. The poor agreement between DMD estimated using AHP-CI-ADF and that measured *in vivo* may have been the result of alkali-peroxide residues in the fibre inhibiting the action of cellulase during incubation. Judkins *et al.* (1990) reported that AHP treatment improved estimates of DMD using ADL. However no other workers have reported a positive effect of this pre-treatment (Cochran *et al.,* 1988; Sunvold and Cochran, 1991; Momont *et al.,* 1994).

ADL marker gave the best estimate of DMD measured *in vivo*, proving superior to all other markers, especially where the quantity of indigestible material in the feed was high. ADL had the further advantage that analysis could be carried-out more rapidly than with the CI-ADF technique and is merely an extension of the routine ADF analysis. The diminishing accuracy of CI-ADF marker as the proportion of indigestible material in the feed increased was probably due to the exhaustion of the cellulase used in the analytical technique. There was no advantage in pre-treating samples with AHP.

3.3: Development of a modified "Tilley and Terry" in vitro digestibility method

3.3.1: Background

Dove and Mayes (1996) have suggested that *in vitro* methods give a more reliable estimation of DMD than internal markers but unfortunately, no end-point, *in vitro* methods have been successfully developed for equids.

The Tilley and Terry (1963) method for determining *in vitro* digestibility of feeds for ruminants is a 2-stage technique that is supposed to mimic the digestive processes occurring within the gut of the ruminant. A sample of feed is first fermented with an inoculum based on rumen liquor. It is then diluted with an artificial saliva solution, and digestion in the abomasum is simulated using pepsin/HCl.

The Tilley and Terry (1963) method does not mimic the digestive processes of the equid very closely. In the equid, pepsin digestion occurs in the stomach before microbial fermentation and most of the digestible nutrients are absorbed before the digesta are subjected to microbial fermentation (Hintz *et al,* (1971). Furthermore, the Tilley and Terry (1963) method relies on rumen liquor as a source of inoculum.

The microbial population of the rumen differs significantly from that of the equine caecum in animals fed the same diet (Kern *et al.*, 1974). Inoculum derived from rumen liquor is unlikely to have the same fermentation characteristics as inoculum derived from equine caecal or colonic liquor. Obtaining donkey-caecal liquor on a routine basis is not possible without access to animals fitted with at least a caecal fistula. However, equine faeces provide a satisfactory alternative to caecal fluid, and have been used successfully as an inoculum for *in vitro* gas production techniques (Lowman *et al.*, 1997) and in the TT method (Whittall *et al.,* 1998).

A further problem associated with trying to adapt the TT method to equid feeds is that extensive recycling of nitrogen occurs in the caecum and colon of equids (Prior *et al.*, 1974). Hintz *et al.* (1971) showed that the nitrogen content of the caecum is frequently higher than that of the terminal ileum, presumably due to the diffusion of urea across the gut wall in to the caecal lumen (Stevens and Hume, 1995). The

standard buffer (McDougall, 1948) used for the TT method contains very little nitrogen, and, therefore, does not mimic the urea-enriched liquor levels in the caecum during fermentation. Use of the McDougall (1948) buffer, where the soluble pepsin-degradable fraction has been removed prior to microbial incubation, is likely to result in a nitrogen-limited fermentation rate, especially with low quality feeds (N. Jessop, Institute Ecology and Resource Management, Edinburgh, Scotland; Personal Communication). The buffer developed for the *in vitro* gas-production technique contains considerable quantities of ammonium hydrogen-carbonate (Theodorou *et al.*, 1994), and, therefore, may be a better choice of buffer than that of McDougall in the TT method.

The following experiment was designed to develop a modified, end-point "Tilley and Terry" method for estimating DMD in equids so that DMD data could be generated from herbage samples in order to calculate DMI at grazing.

3.3.2: Method

Inoculum preparation

Whilst it is sometimes possible to obtain caecal liquor from fistulated ponies, caecally-fistulated donkeys are rarely available. It has recently been shown that equid faeces can be used as an inoculum for *in vitro* gas production techniques (Kirkhope and Lowman, 1997). An inoculum was, therefore, prepared using faeces from either donkeys or ponies; between 1-2 kg freshly expelled faeces were combined with an equal quantity (w/w) of artificial saliva prepared according to Tilley and Terry (1963). The faecal suspension was then crudely homogenised in a domestic blender (Waring) for 30 seconds, placed in an air-tight plastic box and

incubated overnight (12 - 16 hours) at 38°C. The following day, the liquor was extracted from the faeces by straining the faecal suspension through several layers of gauze. The inoculum was prepared by adding the faecal liquor to CO_2-gassed, artificial saliva in the proportion 1:4. The inoculum was gassed with CO_2 and incubated anaerobically at 38°C for up to 1 hour before been added to the substrate.

Incubation order

To try to more closely simulate equid digestion, the Tilley and Terry (1963) method was modified by changing the order in which the 2 incubations were carried out. The food was firstly incubated for 48 hours at 38°C, with 2.0 g/l pepsin in 0.1 N HCl at pH 1.2. The remaining residue was then centrifuged at 1800g for 15 minutes and the supernatant was discarded. The residue was neutralised by adding 2 ml N Na_2CO_3, and 50 ml of inoculum was added. The tubes were gassed with CO_2, sealed and returned to the incubator for a further 48 hours. The remaining DM was then determined and the DMD calculated by difference.

Nitrogen content of inoculum

Discarding the supernatant after pepsin incubation may have affected the degradability of the residue, particularly in respect of low-protein foods, where nitrogen is likely to become limiting, thereby reducing the overall microbial degradation of the diet (Preston and Leng, 1987). Hintz *et al* (1971) showed that the crude protein content of the caecum was frequently higher than that of the ileum, suggesting that there is a source of nitrogen in the caecum other than that derived directly from the diet. This source probably arises through diffusion of NH_4^+ or urea across the gut wall (Nelson and Tyznik, 1968). To try to take account of this additional nitrogen input, a second batch of *in vitro* tests were conducted with the

foodstuffs. The amount of nitrogen in the artificial saliva solution was increased to provide 13.8 mg NH_3/100ml final inoculum. The level of ammonia in the artificial saliva was equivalent to the maximum level of caecal NH_3 measured by Nelson and Tyznik (1968).

Ammonia was added to the artificial saliva solution as ammonium hydrogen carbonate (NH_4HCO_3), so that the buffering capacity of the artificial saliva was not affected; 1g of $NaHCO_3$ was replaced by 0.94g of NH_4HCO_3. In practice the quantities of reagents required to make up 1 litre stock saliva solution were 33.3g anhydrous sodium hydrogen phosphate (Na_2HPO_4), 46.7g $NaHCO_3$, 2.2g NH_4HCO_3 and 32 ml of mixed salt solution (McDougall, 1948). The dilution rates of stock saliva solution were the same as those used by Tilley and Terry (1963).

Comparison of two modified 'Tilley and Terry' in vitro DMD methods with the standard method

A comparison of the original Tilley and Terry (1963) (TT) method with 2 modified methods was carried out with feeds of known *in vivo* DMD. The first modified method used the same artificial saliva solution as suggested by Tilley and Terry (1963), but changed the order of incubation, so that the feed samples were pre-digested with pepsin before microbial fermentation (PP). The second modification used pre-digestion with pepsin and an artificial saliva solution, which, when combined with faecal liquor, provided an inoculum with 13.8 mg/100ml of non-dietary ammonia (PP+N).

The feeds used in the trial were, in the case of ponies, alfalfa, haylage and barley straw, and, in the case of donkeys, alfalfa, haylage, barley straw and a poor quality hay from Zimbabwe (see table 6.2 and 8.1 for chemical composition details). Two sets of duplicate samples of each food were digested *in vitro* using each of the 3

methods described above. One set of samples was digested with inoculum derived from pony faeces, the other with inoculum derived from donkey faeces. Two blank tubes for each method and each inoculum were included in the experiment so that any contribution of the faecal liquor micro-organisms to the final residual dry matter could be calculated.

3.3.3: Results

Comparison of the values obtained with 3 *in vitro* methods for estimating DMD with values obtained *in vivo* (Table 3.3) showed differences between the 3 *in vitro* methods. All 3 methods provided closer estimates of *in vivo* DMD for ponies than for donkeys (Table 3.3).

The original TT method was the most unreliable, consistently under-estimating *in vivo* DMD for all 3 feeds for ponies and all 4 feeds for donkeys; the method also had the lowest r^2 values of the 3 methods tested. The PP method provided the closest estimate of *in vivo* DMD of alfalfa for both ponies and donkeys. However, as the DMD of the feed decreased, the PP method became less reliable; for ponies the r^2 (0.96) was only slightly higher than that for the TT method (0.95) but considerably higher in the case of the donkeys (0.84 compared with 0.76). Overall, the PP+N method provided the most reliable estimates of *in vivo* DMD, despite a tendency to underestimate the DMD of alfalfa. The r^2 value of this method was the highest of all 3 methods tested (0.99 in ponies and 0.93 in donkeys).

Table 3.3: Comparison of mean *in vitro* estimation of DMD (with s. e.) obtained using Tilley and Terry (TT), pepsin pre-treatment (PP) and pepsin pre-treatment plus added NH_3 (PP+N) methods with *in vivo* values of three foods fed to ponies and four fed to donkeys

	In vivo	*In vitro* methods		
		TT	PP	PP+N
Pony				
Alfalfa (n=4)	0.75 (0.015)	0.59 (0.012)	0.73 (0.015)	0.67 (0.014)
Haylage (n=4)	0.52 (0.010)	0.31 (0.006)	0.43 (0.009)	0.42 (0.009)
Straw (n=4)	0.44 (0.009)	0.08 (0.001)	0.19 (0.004)	0.30 (0.006)
r^2 (n=12)		0.95	0.96	0.99
Donkeys				
Alfalfa (n=4)	0.72 (0.016)	0.41 (0.009)	0.72 (0.015)	0.70 (0.014)
Haylage (n=4)	0.53 (0.003)	0.29 (0.003)	0.43 (0.002)	0.40 (0.002)
Straw (n=4)	0.52 (0.003)	0.06 (0.001)	0.16 (0.000)	0.24 (0.002)
Zimbabwe hay (n=4)	0.42 (0.002)	0.04 (0.000)	0.15 (0.001)	0.16 (0.001)
r^2 (n = 16)		0.76	0.83	0.93

Figure 3.2: Relationship between in vivo DMD values of 3 feeds (alfalfa, haylage and barley straw) fed to ponies and values obtained with three in vitro DMD methods; (Tilley and Terry (TT), pepsin pre-treatment (PP) and pepsin pre-treatment with added NH_4HCO_3 (PP+N)).

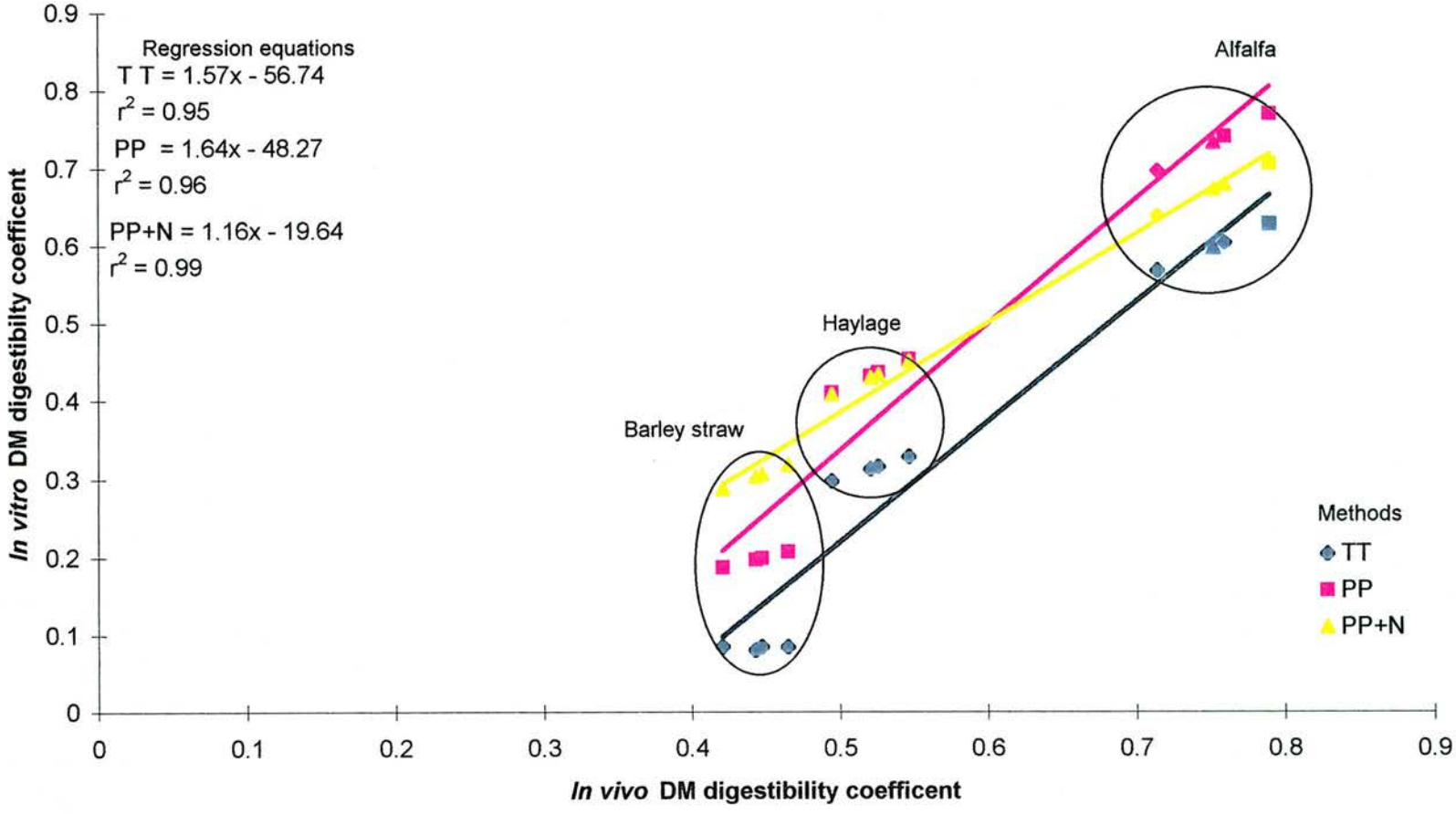
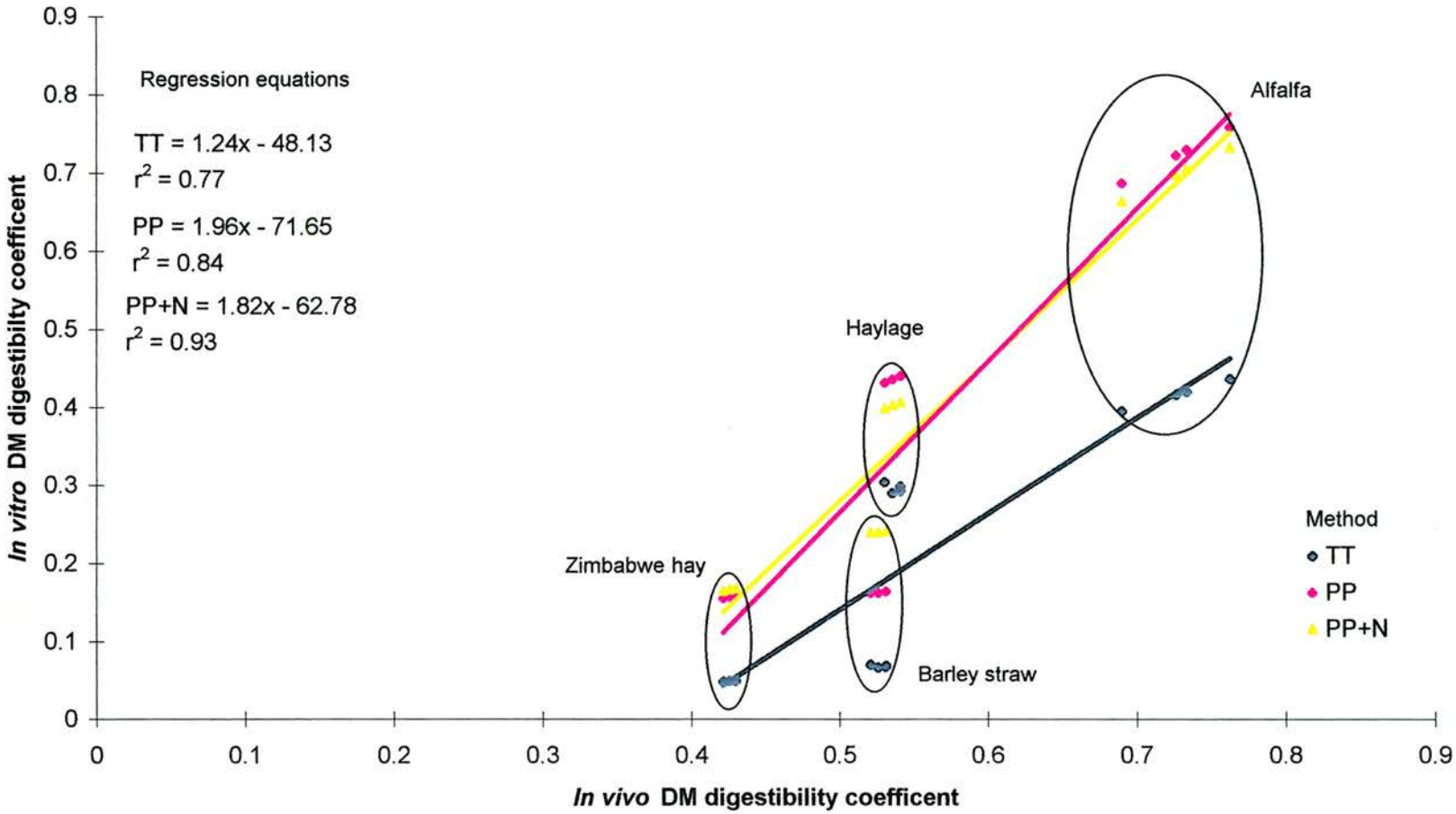


Figure 3.3: Relationship between in vivo DMD values of 4 feeds (alfalfa, haylage, barley straw and Zimbabwe hay) fed to donkeys and values obtained with three in vitro DMD methods; (Tilley and Terry (TT), pepsin pre-treatment (PP) and pepsin pre-treatment with added NH_4HCO_3 (PP+N)).



All three *in vitro* methods tended to underestimate *in vivo* DMD of the more fibrous feeds (Table 3.3). Both pepsin pre-treatment and addition of NH_4HCO_3 to the inoculum buffer reduced the difference between *in vivo* and *in vitro* estimates of the DMD values of these feeds.

The regression equations derived for each *in vitro* method are shown in Figures 3.2 and 3.3. For both ponies and donkeys the regression equation for the PP+N method had a higher r^2 value, lower intercept and slope closer to parity than the other 2 *in vitro* methods.

3.5.3: Discussion

The data points provided by the *in vitro* determination of DMD using the TT, PP and PP+N method were few and inferences must be drawn with care. However, the data obtained gave some indication of the relative reliability of the 3 *in vitro* methods.

Faecal inoculum

The experiment showed that fresh faeces can be used as a source of micro-organisms to provide an inoculum for *in vitro* fermentation. Compared to donkey faeces pony faeces gave *in vitro* estimates of DMD closer to those measured *in vivo*. This may have been due to the length of time between the voiding of faeces and their collection. In the case of the pony inoculum, faeces were collected when eliminated and, within a few minutes, placed in a warm anaerobic environment. In the case of donkeys, there was a delay of approximately 30 minutes between the elimination of the faeces and placement in a warm anaerobic environment.

Although further experimentation was desirable, it appeared that faecal inoculum derived from freshly voided faeces kept in warm anaerobic conditions was an effective inoculum.

Pepsin pre-treatment

Pepsin pre-treatment was shown to give closer estimates of *in vivo* DMD in equine diets than did pepsin post-treatment given in the non-modified TT method. For diets with high DMD and digestible crude protein, such as alfalfa, the PP method give better results than the PP+N method. This is probably because the nitrogen content of the feed was sufficiently high not to limit the fermentation rate. In the lower-quality feeds tested in this experiment, such as straw and poor quality hay, PP gave more reliable estimates of *in vivo* DMD than did the TT method but was not as reliable as PP+N. With moderate quality haylage, both PP and PP+N methods tended to underestimate DMD to a similar degree, although the PP+N method had a higher r^2 value.

Increasing the nitrogen content of the inoculum buffer

The addition of nitrogen, in the form of NH_4HCO_3, to the inoculum improved estimates of *in vivo* DMD of low and medium quality feeds. In the case of alfalfa, the PP+N method underestimated the *in vivo* DMD to a greater degree than did the PP method. This may have been because additional N resulted in NH_4^+ concentrations exceeding those required for optimal fermentation, leading to inhibition of micro-organism activity.

The results of this experiment suggested that the amount of NH_4HCO_3 that should be added to the inoculum buffer solution depends largely on the quality of the feed, and, in particular, the soluble nitrogen concentration. Addition of NH_4HCO_3 should

be sufficient to prevent microbial processes from being rate-limited by lack of nitrogen, but not so excessive that NH_4^+ concentrations become inhibiting, as may have been the case with alfalfa. The precise calculation of the amount of NH_4HCO_3 to add to the buffer solution requires a knowledge of the soluble nitrogen content of the feed, the amount of nitrogen digested during the pepsin pre-treatment and the optimum NH_4^+ concentration of the fermentation liquor.

It appears from this experiment that, in the case of the straw and hay feeds, the amount of NH_4HCO_3 included in the buffer solution used for the PP+N method was not enough to provide the microbes with sufficient nitrogen for optimal fermentation. Further *in vitro* studies are required to establish the amount of NH_4HCO_3 that should be added to the buffer solution to optimise the fermentation process.

3.6: Conclusions

1. A rapid method for simultaneously dosing Cr_2O_3 and C_{36} external markers for both donkeys and cattle was developed. Rapid dosing of external markers allows the dosing frequency to be increased, leading to less circadian variation in faecal marker concentrations and more accurate estimates of FO. Dosing 2 different markers allows estimations of FO to be cross-checked, thereby improving the validity of the results
2. Using ADL as an internal marker gave the best estimations of DMD in ponies, donkeys and cattle receiving 3 diets containing different amounts of indigestible material.
3. A modified 'Tilley and Terry' *in vitro* method that gave reliable estimates of DMD in typical equine diets was developed. The method involved pre-treating feeds with pepsin and enriching the inoculum buffer with NH_4HCO_3 in an effort to more accurately mimic the equine digestive processes, thereby giving better estimates of DMD.

CHAPTER 4

METHODS FOR THE COLLECTION OF FEEDING BEHAVIOUR DATA

4.1: Introduction

Study of the feeding behaviour of free-ranging herbivores provides valuable indicators of the condition of the available forage resource. Time budgets and circadian distribution of feeding activity are particularly useful parameters for comparing different classes of herbivore and seasonal changes in forage resources. However, collection of feeding behaviour data, in order to compile time budgets and circadian patterns, is labour-intensive during both its collection and subsequent processing. True behavioural observations are made more difficult by the need for human observers to approach close to the animals, which may disrupt natural behaviour. The process of carrying out behavioural studies of free-ranging animals would be made easier if data collection and, or, processing were automated to some degree.

This project investigated 2 ways of automating behavioural observations with the aim of reducing labour intensity, preventing animal interference, computerising record keeping and evaluating method development. Firstly, a method was developed that allowed the electronic recording of the behavioural data obtained by observers using a personal, hand-held computer. Secondly, existing automatic methods of recording feeding behaviour without the need for human presence in the field were investigated and developed. This section presents the findings from these studies.

4.2: *Electronic recording of behavioural data collected by scan sampling techniques*

4.2.1: Background

The scan technique of recording behavioural data involves taking a 'snap-shot' observation of an animal's behaviour at a pre-set time interval, usually every 5 or 10 minutes. The method is generally employed to record types of behaviour that are sustained for extended, uninterrupted periods, such as feeding or rumination. Other behavioural events of short duration, such as drinking or defaecating, cannot be recorded reliably with the scan technique, and are best assessed using focal observational methods. Several animals can be observed simultaneously using the scan technique, allowing direct comparisons of time budgets and behaviour patterns of different animals under identical environmental conditions.

The traditional methods of recording scan observations in the field usually involve little more than a paper-recording grid, pencil, timing device and clipboard. This method has the advantage that it is simple to operate and presents few technical difficulties. However, implementation in the field can be problematic because:

1. errors in recording observations on the grid when several animals are being observed, effectively limiting the number of animal that can be observed simultaneously;
2. difficulty in operating a paper-based system outdoors in wet and windy conditions;
3. possible disturbance of animals when turning papers between observations;
4. problems in following animals under rangeland conditions carrying recording equipment and operating a timing device;
5. errors during manual summation of data.

Whilst none of these problems is insurmountable, the use of electronic recording requires less effort to operate in the field, so allowing individual observations to be made more quickly, more attention to be paid to the animals under observation and more animals to be observed simultaneously. Subsequent data-processing of electronic records is easier since data files can be analysed by computer with spreadsheet software. Drawbacks of electronic recording include the risk of data loss through power failure and possible errors in data recording due to mis-keying.

4.2.2: Development of recording technique

Design

Demment and Greenwood (1987) developed the concept of electronic recording of behavioural data in the early 1980's using a laptop computer recording data onto magnetic tape. More recently, the development of hand-held, data-logging devices such as the Psion Organiser LZ64, has allowed the development of portable recording systems that can be easily used in the field (Jarvis and Cockram, 1995).

The Psion Organiser LZ64 (PO), is a small hand-held device (250g in weight and 140x75x30 mm in size) powered by a 9v battery, which allows continuous data collection for several hours (Plate 4.1). The PO has a small liquid crystal display (LCD) screen (20 characters wide by 4 high), allowing the presentation of scrollable data and menu screens and can store up to a maximum of 32,000 bytes of data on removable storage devices. Data from the PO can be downloaded via a communications link cable onto a personal computer, where data files can be then immediately read using spreadsheet software packages such as Microsoft Excel or Lotus 123. The PO has a built-in programming language called OPL, that can be used to present the users with menu options and send data inputs to storage devices.

The PO has several built-in functions, the most useful of which is a system clock which can automatically record time, day and date information.

The objective was to develop a menu-driven OPL program that could be used to record behavioural data in the field. The design criteria were:

1. a built-in timer that would signal the user to make a data entry after the desired scan interval had elapsed;
2. a rapid recording system involving as few keystrokes as possible;
3. flexibility in terms of comments and activity descriptions recorded;
4. simultaneous recording of behaviour for up to 12 animals;
5. easy-to-follow menu instructions that provided the user with flexibility in terms of the number of animals observed;
6. file management and data reviewing facilities;
7. rapid, automated data processing.

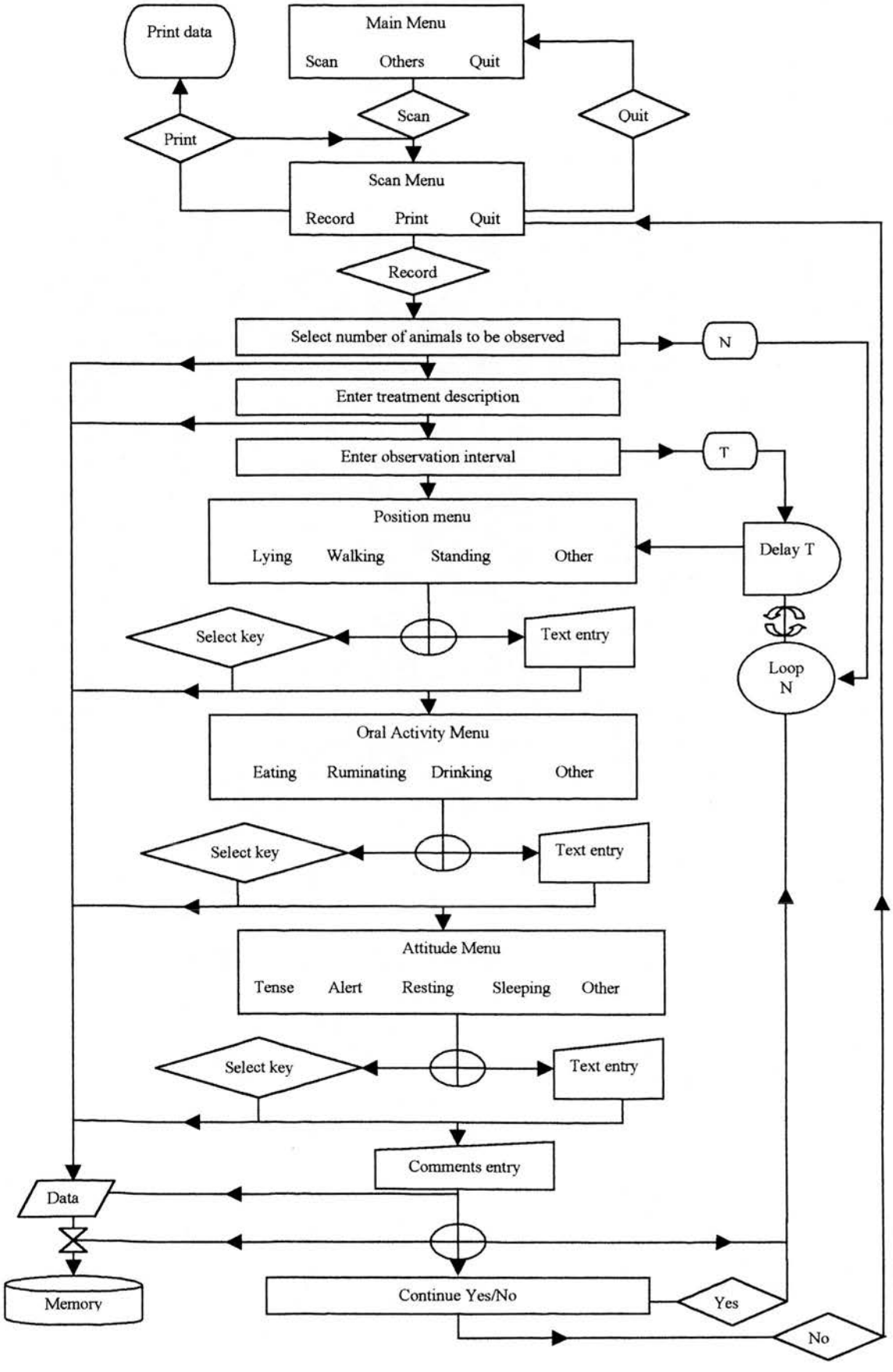
Time intervals between scans

The PO has an internal clock that can be used to provide time, day and date information to time-reference the data. This feature was used to produce an integrated countdown-timing device within the OPL program.

On initiating the program, the user entered the time interval between observations in minutes. After the allotted time interval had elapsed the PO emitted several beeps, and then displayed the first behavioural data menu. The observer then entered one of the menu option. A similar procedure was followed for the second and third menu screens (Figure 4.1). After entering the comment statement, the behavioural data, comments, animal identification, time (to the nearest second), and date were recorded automatically on the data storage device.

Plate 4.1: Hand-held computer (Psion II LZ64) used to collect behavioural data

Figure 4.1 Algorithm for the behavioural data collection program



Rapid recording of behavioural data

The PO had limited memory storage capacity (128K), and each behavioural data entry had to be kept as short as possible to reduce memory demands. For this reason, a category system was developed that provided a text-string describing the position, attitude and oral activity of an animal and occupying 30 bytes of memory space; this allowed ~1000 single data entries to be made before downloading was necessary. It would have been possible to reduce the memory requirement still further by using a code rather than text description. However, it was felt that the code option would reduce the flexibility of the system and make in-field data checks more difficult.

To facilitate rapid data collection, behavioural activities were divided into 3 categories as described by Pearson and Smith (1994). These categories were 'position', 'oral activity' and 'attitude'. Within these categories, short lists of the most common behavioural activities were compiled. All activities in a single list were mutually exclusive of one another (i.e. a list could not include 2 items that could occur simultaneously). Each category included the list item 'other' enabling the observer to describe any activity that was not referred to explicitly in the list. In the OPL program each category heading appeared as a menu heading. Under each category menu there was a list of items that corresponded to the items in the prepared category list (Figure 4.1). To record the behaviour of an animal under a given category, the observer simply pressed the key on the PO which corresponded to the first letter of the list item (e.g. under the position menu, 'standing' would be recorded by pressing 'S').

The program went through each category menu in the sequence shown in Figure 4.1. After completing the recording sequence, the observer was given the opportunity to

enter a 60-character comment about the observation. If the behaviour exhibited by the animal was not described by any of the categories in each menu, the observer could enter a 15-character description of behaviour before proceeding (Figure 4.1). Using this system, the majority of common behavioural patterns of a single animal could be recorded by pressing 4 keys in sequence in less than 1 second. After the data entry for this animal, the program went on to display the next animal menu options. With this method, the behaviour patterns of 12 animals could be recorded in very rapid succession; the time between observations being limited by the time taken to make an observation, rather than the time taken preparing to record the next observation.

Flexibility of program

The OPL program offered observers flexibility in several ways. Firstly, the observer set the number of animals that were to be recorded simultaneously at the beginning of the observation session. From a menu of options, the observer could record up to 12 animals, select a group of animals, or a single animal. The subsequent menu allowed descriptive information about the observation group to be entered.

Further flexibility was offered by the option to record *ad hoc* short comments under the 'other' item in each menu and more detailed remarks at the comment text entry stage.

The program could be aborted at the end of any observation run, and parameters such as observation interval or treatment description be reset without the existing data being overwritten.

File management and data checking

The existing file management and data checking facilities of the PO were found to be adequate and needed no modification.

Data processing

Data processing was carried out after the files had been downloaded on to a personal computer (PC). The PO produced a text file in ASCII format for each animal observed during the observation sessions and these files were downloaded on to a PC at the end of each observation session. The ASCII files could be checked for errors using any word processing software e.g. initial data processing was carried out using macros written for Microsoft Word, version 6 (MSW6) and data were then summated using Microsoft Excel version 5 (MSE5).

4.2.3: Evaluation of electronic recording of behavioural data.

The behavioural data collection program was used successfully to collect data in both Ethiopia and Zimbabwe. It was found to be a highly flexible system that simplified data collection in the field and reduced the amount of time subsequently spent processing results. The following summarises the benefits and problems associated with the system.

Advantages

The observer was able to follow the animals more attentively than when using paper-based methods and caused less disturbance to the animals. The PO was made weather-proof by placing it in a plastic bag, through which the keys could be pressed. Simultaneous observations of up to 12 animals could be made. This was particularly helpful when observing cattle that remained in close proximity to each other and had

closely synchronised behaviour. Under ideal circumstances, observations for 12 animals could be recorded in less than 30 seconds.

Data processing could be carried out more rapidly using the automated system as all stages of data collection were preserved on file. During the process, error-checking was made simpler and corrections readily made. The comment facility of the program allowed any recording errors to be easily noted and tracked, together with the data entry.

The training required to operate the PO in the field was minimal although the downloading process was a little more complex.

Disadvantages

The disadvantages to using the PO to collect data were mainly logistical and could be overcome by good planning. The power demands on the PO were unpredictable, and interruption of data collection was usually due to battery failure. This was readily overcome by providing the observer with 2 back-up batteries. The use of rechargeable batteries minimised battery expense. A total of 6 batteries where used in rotation as recharging took at least 24 hours. Rechargeable batteries had the disadvantage that a fairly constant supply of mains-electricity was required. This proved problematic in Ethiopia where the supply was erratic. Non-rechargeable batteries that fitted the PO were, however, readily available at village stores and could be used when the absence of mains power prevented the use of rechargeable batteries.

The PO required downloading every 2-3 hours preventing continuous observation over 24 hours. Downloading the PO in the field was possible by laptop computer but delayed the onset of the next observation session by about 15 minutes.

4.3: Automatic recording of grazing behaviour

4.3.1: Background

There have been many attempts by pasture research scientists to develop equipment that can automatically record the grazing behaviour of free-ranging herbivores. Amongst the earliest papers that appeared on the subject were those of Canaway, Raymond and Taylor (1955); Duckworth and Shirlaw (1955); and Balch (1958); methodologies were reviewed by Penning (1983). The attraction of such systems are that a detailed knowledge of feeding behaviour can be acquired without the need for labour-intensive, behavioural observations or for human observers to be in close proximity to the grazing animal.

Early methods used the vibra-recorder; an instrument that recorded the head movement of grazing animals (Allden, 1962). More recently, and especially since the advent of microelectronics, techniques have been developed that monitor the jaw movements of animals and provide a less equivocal indication of when grazing actually occurs. Technical developments have focused on 2 particular problems of automatic recording of grazing behaviour: i) the detection of jaw movement; and ii) the method used to collect and record the behavioural data.

Detection of jaw movement

Several methods for detecting jaw movement have been developed, including simple switches (Chambers, Hodgson and Milne, 1981) and strain gauges (Beauchemin, *et al.*, 1989). However, the 2 most common methods depend on a pneumatic system, originally used by Welch and Smith (1969), and a variable resistance system developed by Penning (1983).

The transducer used in pneumatic systems was a foam-filled, small balloon fitted below the chin of the animal with the aid of a halter (Plate 4.2, 4.3, and 4.4). Air was expelled from the balloon when the animal opened its mouth. The pneumatic compression generated by each mouth movement was conducted by way of a flexible tube to a counting device that detected and recorded each pulse (Plate 4.3). This transducer has proved to be reliable over several decades of research into feeding behaviour and has been incorporated into a commercially available device (Brouillette, Pell and Welch, 1993).

More recently, Penning (1983) developed a resistive-noseband transducer, a graphite-filled rubber tube that detects the change in electrical resistance when stretched as the animal bites. This transducer has the advantage over the pneumatic transducer that jaw movements are directly converted into electric signals measurable by electronic devices. Furthermore, the response of the transducer is proportional to the degree of jaw movement, giving additional information about the nature of the bite. Several pasture research groups have used the method to monitor feeding behaviour in horses, cattle and sheep (Myers, 1994; Matsui and Okubo, 1991a,b, Rook and Penning, 1991a,b).

Both these jaw movement transducers have been developed for temperate pasture conditions and have not been tested under the more arduous, rangeland conditions of the semi-arid tropics. An objective of the current project was to test both methods and, if necessary, modify them for rangeland conditions.

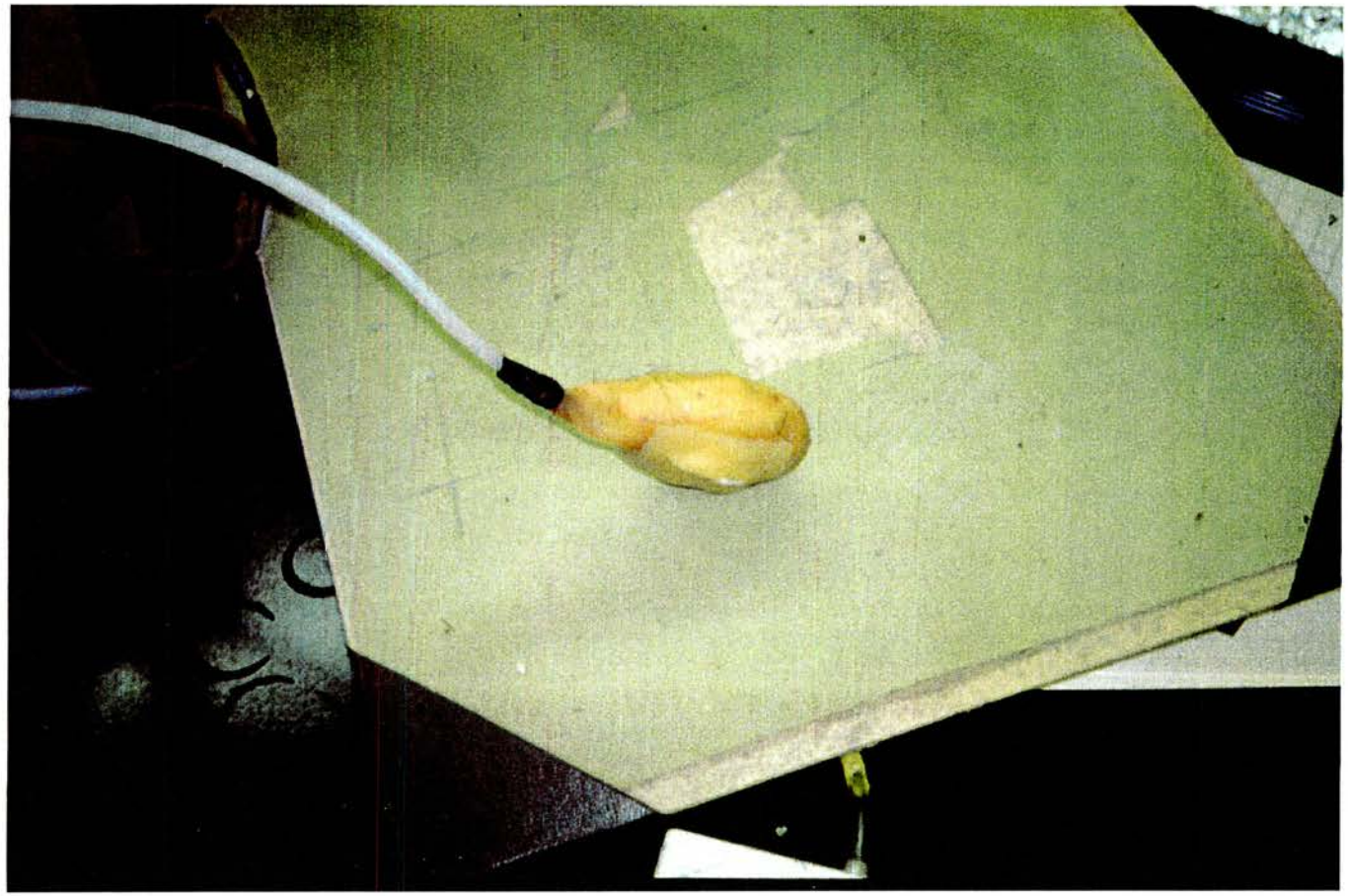


Plate 4.2: Foam filled balloon used as a transducer to detect jaw movements in the IPRED bite meter

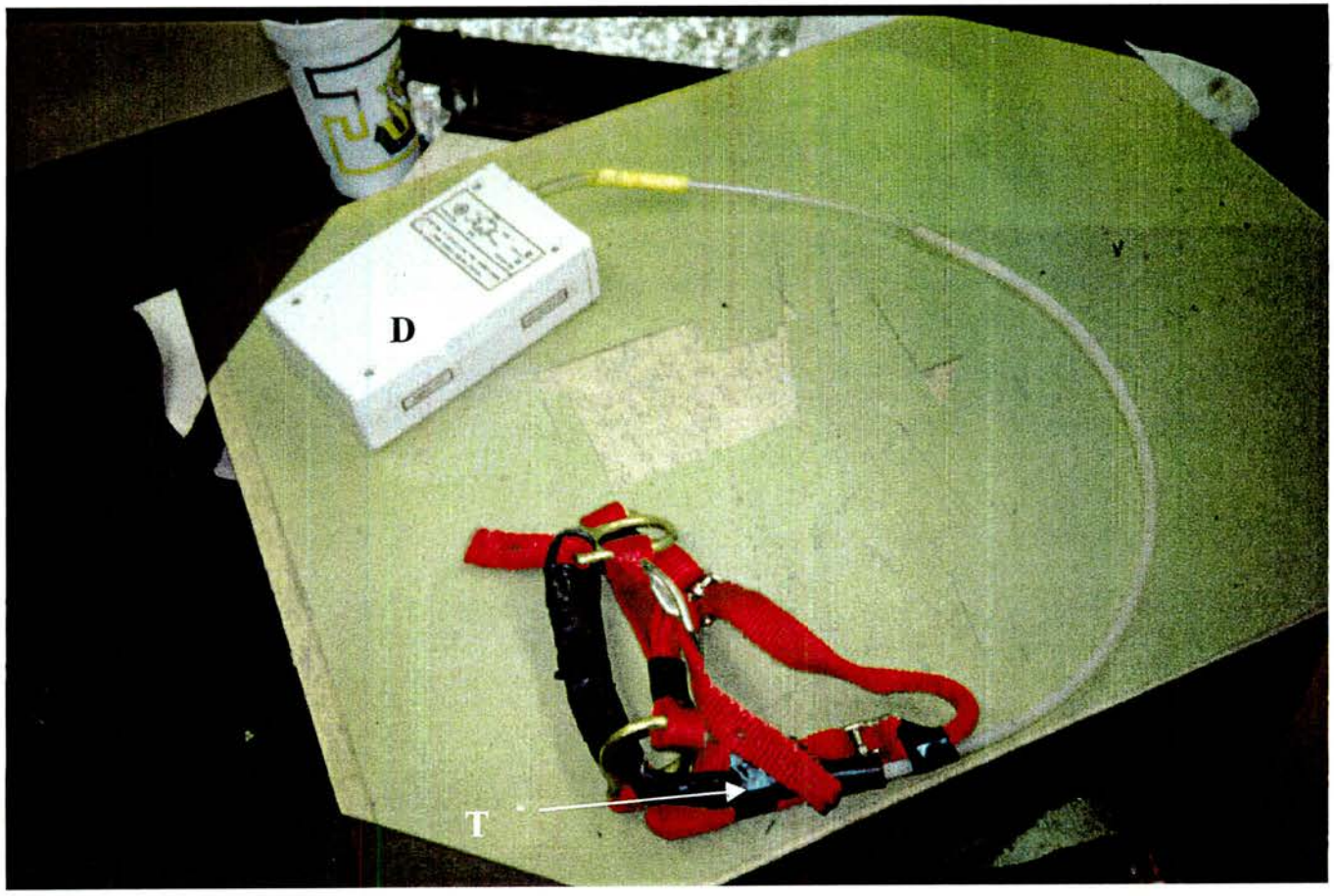


Plate 4.3: Halter adapted for small ruminants fitted with transducer (T) and plastic tube leading to IPRED data logger (D)

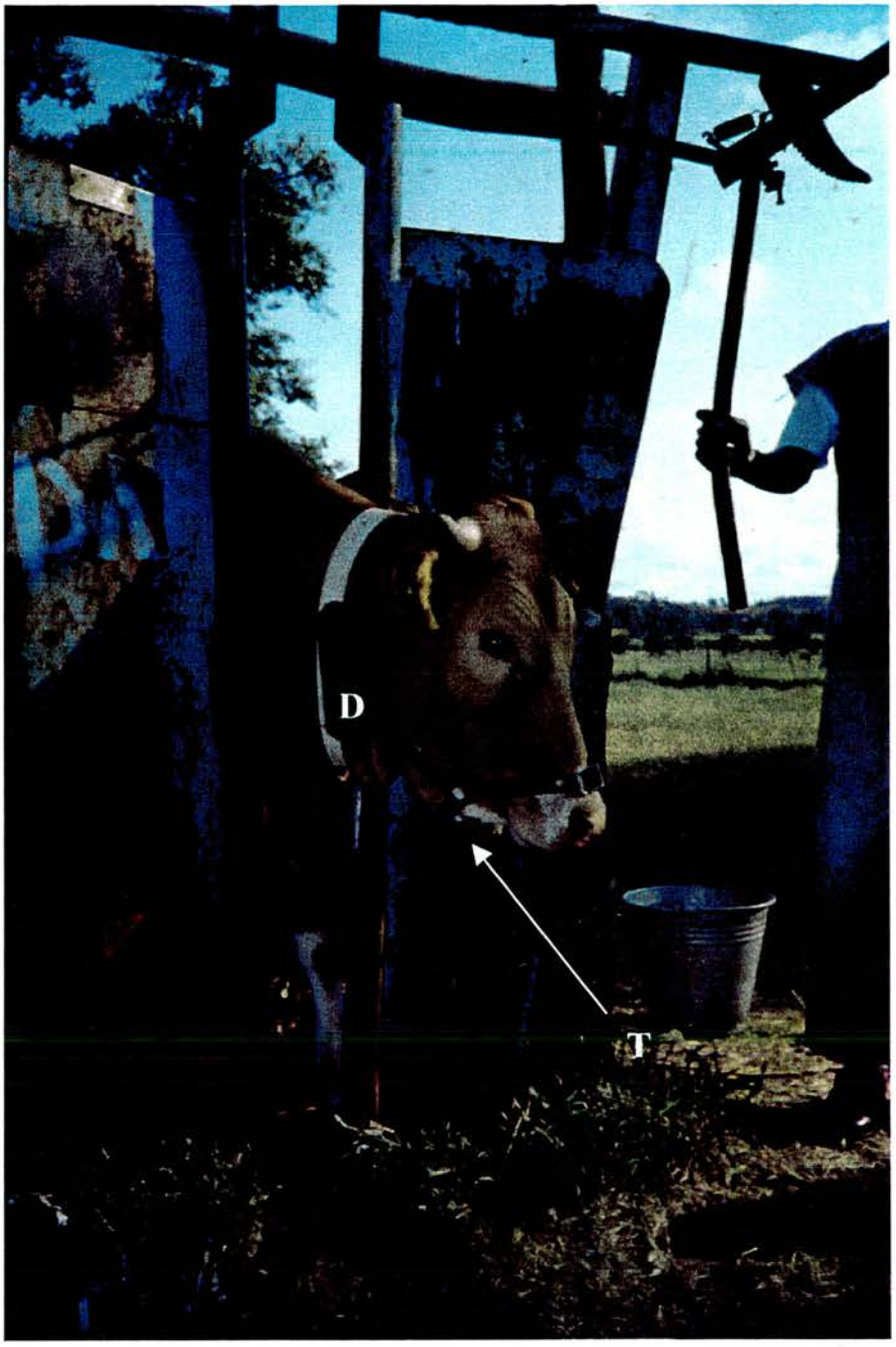


Plate 4.4: Bite meter halter arrangement modified for cattle with IPRED data logger (D) fitted to halter and transducer (T) fitted under lower jaw

Data collection and storage

The signals produced by jaw movement transducers, of whatever design, produce a vast amount of data (20 MB per day) that must be recorded and processed by some means or other (P. R. Lawrence, University of Hohenhiem, Stuttgart, Germany; personal communication). Two recording and processing options are available: i) devices that process raw signal inputs and store data within the equipment carried on the animal or ii), devices that send the raw signal telemetrically from the animal to a remote receiver attached to a computer.

Originally, the raw output from graphite 'tube-type' transducers was recorded on magnetic tape with the aid of a modified portable tape-recorder (Penning, 1983). This system allowed 24 hours of behavioural data to be collected (Huckle, Clements and Penning, 1989). The use of tape-recorders in the field is not very practical under rangeland conditions because of the risk of mechanical and power failures. More recently, solid-state, datalogger systems for recording data have been developed (Matsui and Okubo, 1991a). These systems have the advantage that they have no moving parts and demand little electrical power. For example, Matsui and Okubo (1991b) developed a system that could continuously record 22 days of behavioural data at grazing.

Digital recording of raw signal outputs is not feasible because the amount of data produced over a 24-hour period exceeds the memory capacity of currently available, solid-state, dataloggers (P. R. Lawrence, University of Hohenhiem, Stuttgart, Germany; personal communication). With datalogger systems, raw signals have to be processed in some way to reduce the amount of data that has to be recorded,

inevitably leading to a permanent loss of some raw data. Moreover, this process relies on an automated and unverifiable decision about what data should be stored.

Several methods of on-animal data processing have been developed but there is considerable variation in the parameters recorded by the different methods. The various systems of Matsui and Okubo (1989, 1990, 1991a, 1991b) processed data to provide a variety of parameters summed over 1 minute. These included number of jaw movements, number of pauses between jaw movements, number of pauses between jaw movements greater than 3 seconds and interval between 2 successive jaw movements. The datalogger system of Brouillette *et al.* (1993) recorded the number of successive 2.5-second sampling periods in which jaw movement did or did not occur. In practice, a balance has to be struck between the amount of memory available, the desired resolution of the behavioural data and the period of time over which data are collected.

Telemetric systems for sending raw data from jaw-movement transducers to a remote data collection system have the advantage that data can be stored on computer hard-disk, giving a much larger memory space compared to datalogger memory chips. Although computers usually process the data, raw signal outputs are not discarded and can be checked manually if necessary at a later date.

The use of telemetry to monitor jaw movement was first attempted by Nichols (1966) with sheep and the principle has been revived on several occasions since then. Rugh (1970) developed a short-range telemetric system for use with rats, and Horn (1981) developed a telemetric system that could be used to monitor the live weight of grazing cattle. McCracken (1992) and Myers (1994) both used telemetric jaw-movement monitors to study the behaviour of grazing horses. On the whole,

however, telemetric systems for data acquisition have not been as widely adopted as datalogger systems.

4.3.2: Design criteria

The concept of a reliable remote method for automatically monitoring the feeding behaviour of grazing animals is an attractive proposition for pasture research scientists. Such a system would reduce the labour-intensive nature of behavioural observations and allow the feeding behaviour of animals to be monitored without the close proximity of humans.

However, total reliance on automatic methods for monitoring feeding behaviour would require systems having the following features:

1 automated data analysis that provided reliable measurements of behavioural parameters such as time spent grazing, bite and chew rates etc;

2 jaw movement transducers that were robust and readily adjusted to fit animals of various sizes and shapes;

3 a lower labour demand than that of non-automated systems, both at the data collection and data processing stages;

4 the provision of unequivocal results with a very high correlation with results obtained using manual methods;

5 very high reliability, so that observation sessions could be planned with confidence to fit within experimental protocols.

If an automated system of feeding behaviour fails to fulfil any one of the above criteria the value of such a system as a 'stand-alone' tool for investigating feeding behaviour is questionable.

4.3.3: Objectives

Two automated systems for monitoring feeding systems were evaluated and developed during the current project: 1) a prototype telemetric system with resistive noseband-transducer and 2) a commercially available, datalogger system with pneumatic transducer.

These systems were evaluated against the design criteria stated above and, where possible, modified to improve their compliance with the design criteria. Once modification was complete, the reliability of each system was tested against manual systems of recording behavioural observations.

4.3.4: Evaluation of a telemetric method

One of the aims of the present project was to develop and evaluate a telemetric jaw movement monitor that could be used to record several animals simultaneously at a distance of 1 km. The choice of a telemetric system over a datalogger system was influenced by the desire to distinguish bites from chews and the need to obtain data with a high degree of resolution. The need to distinguish bites from chews also influenced the choice of resistive noseband as the jaw movement transducer.

System description and development

The telemetric system named HORAS was developed from the systems described by McCracken (1992) and Myers (1994). The HORAS system developed for use in this project was designed and built by Dr. H. Brash, of the Department of Medical Physics, University of Edinburgh. The system described by Myers (1994) was developed so that data could be gathered simultaneously from 4 animals.

The receiver unit consisted of 4 receiver modules, an ADC and a portable computer, weighing ~15 kg (Plate 4.5). The transmitter units fitted to each animal consisted of

an aluminium cylinder 100mm in diameter and 200mm long, weighing 700g, with a 100mm flexible antenna protruding mid-way along the longitudinal surface of the cylinder. The transmitter unit was fitted to the animal with the aid of a halter, under the head of the animal between the jawbone and the top of the neck (Plate 4.6 and 4.7). The complete head-harness arrangement weighed 1.2 kg. The system used a licence-exempt frequency of 458 MHz, with a transmitting power of 25mW, in theory providing a range of 1 km.

Once decoded, the digital signal from each transmitter device was displayed simultaneously on the receiving computer screen. Data from each transmitter were also stored on the computer hard disk. The original signal from each transmitter could be replayed in part or completely once data collection was complete.

Rangeland trial

Initial testing of the equipment under rangeland conditions in south-eastern Ethiopia gave very poor results. The signal from the transmitters had a range of only 20m whereas the same transmitter equipment in the UK had a range of at least 1000m. The reason for this equipment failure in Ethiopia may have been due to interference from other signals on a similar frequency or poor antenna performance on the transmitter or receiver.

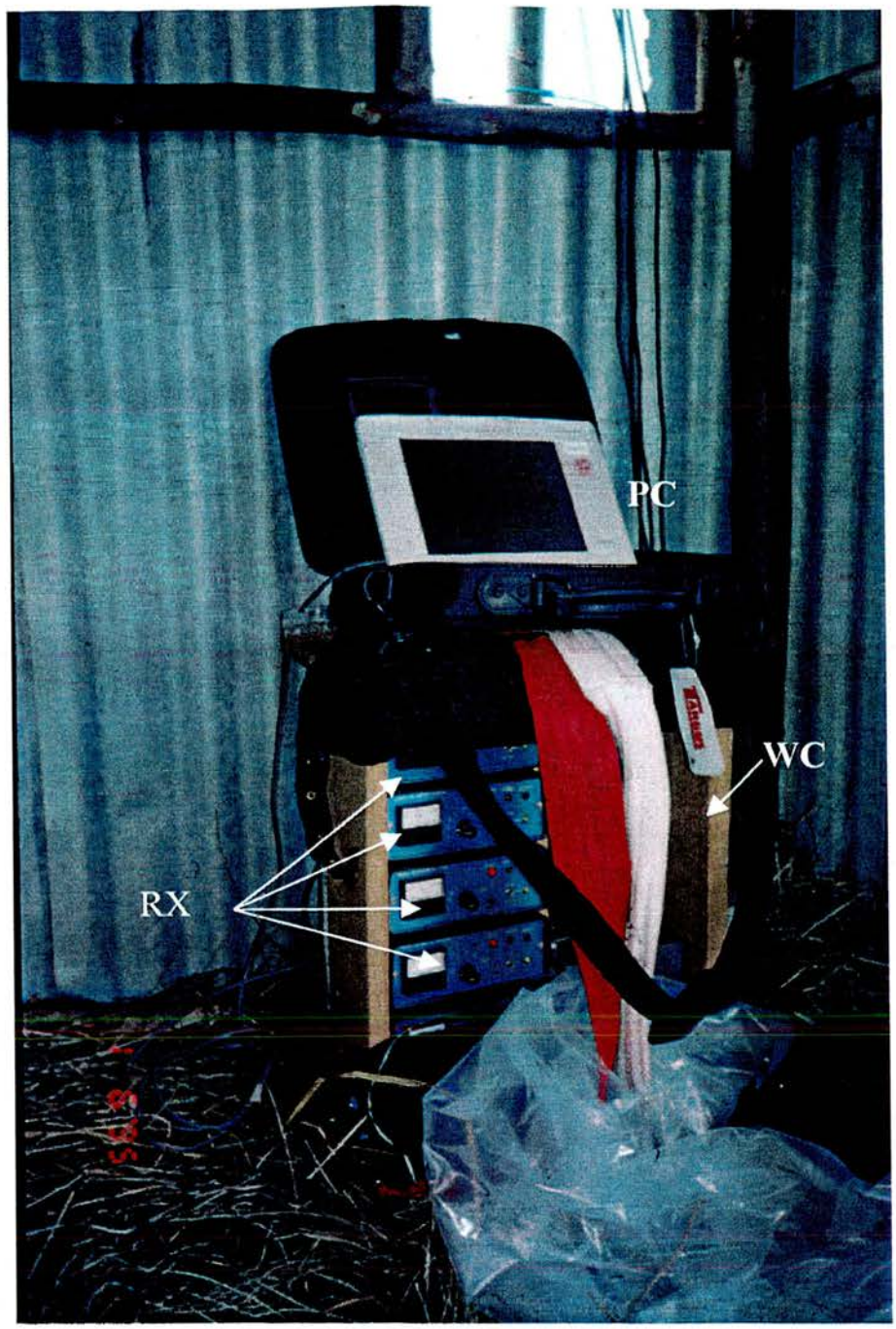


Plate 4.5: Receiving equipment for the telemetric bite meter, showing portable personal computer (PC), four receiving units (RX) and wooden carrying frame (W)

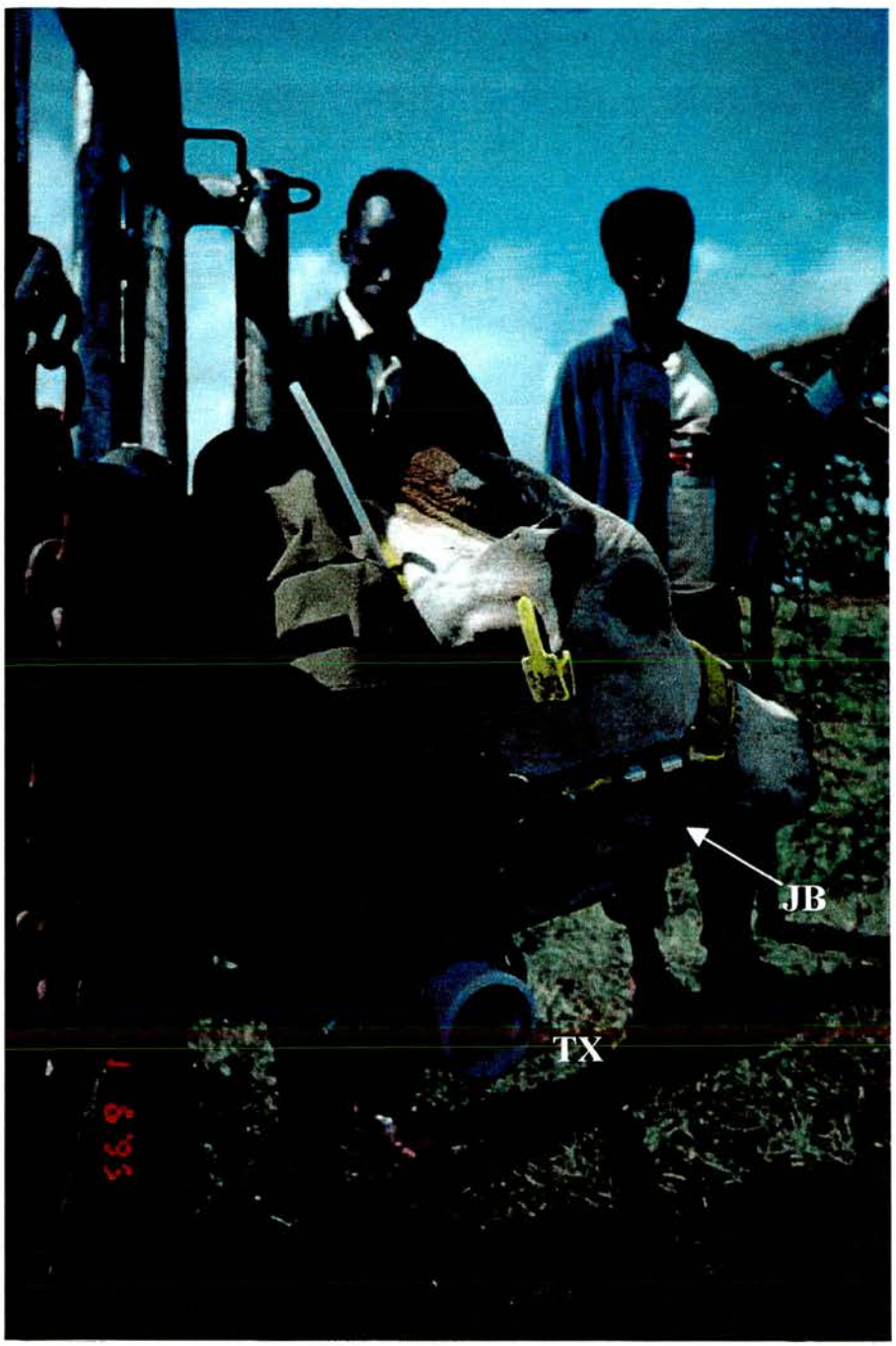


Plate 4.6: Telemetric transmitter (TX) fitted with resistive jaw band transducer (JB)

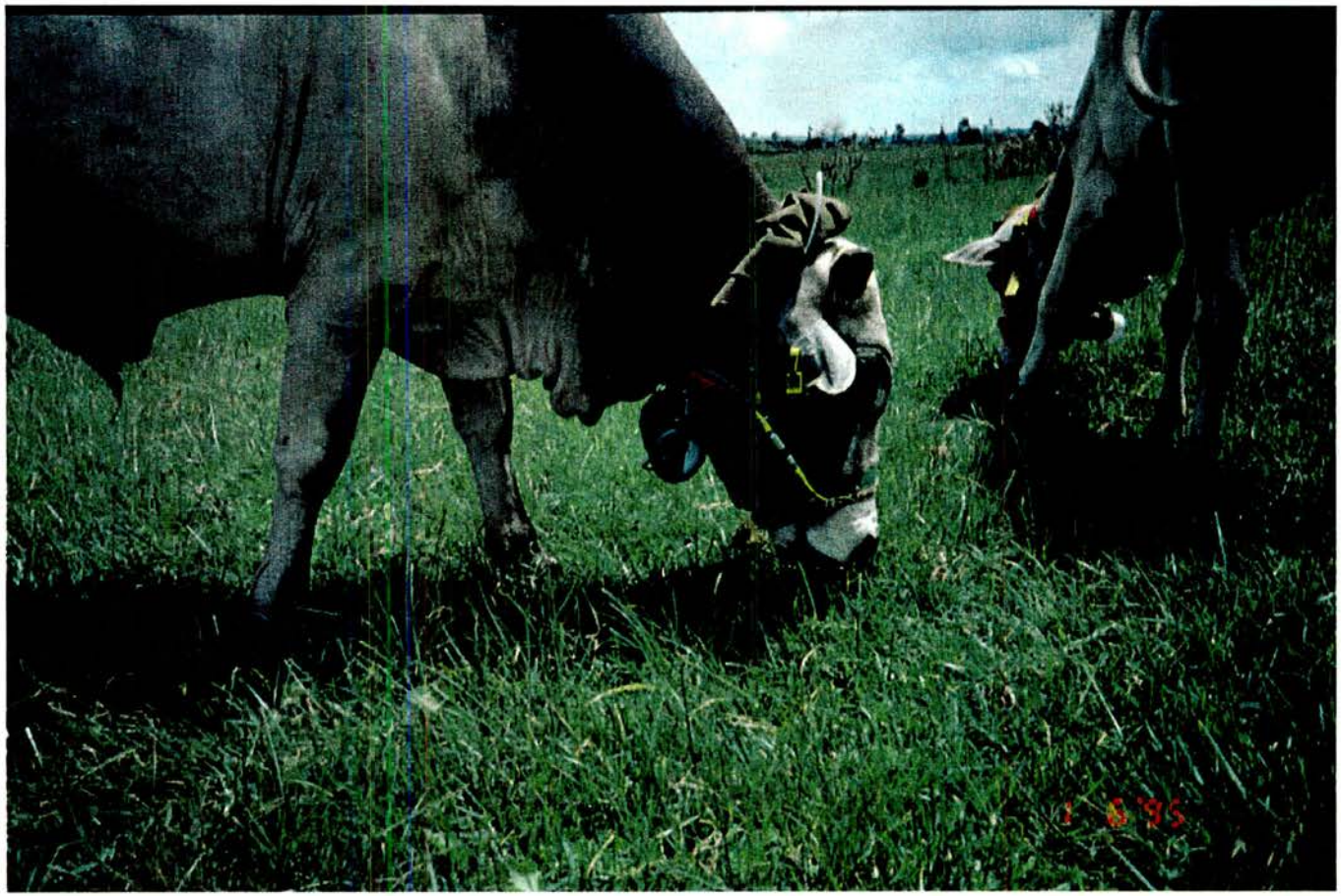


Plate 4.7: Ogaden cattle fitted with telemetric bite meters grazing *Pennisetum clandestinum* dominated pastures in South-eastern Ethiopia

Improvements to the receiving antennae were made by mounting them on a 0.3m square aluminium earth plate that could be held 3m above ground level with the aid of a wooden pole. Transmitter antennae were improved by replacing the short wire antenna that hung from the bottom of the transmitter cylinder with a rigid antenna that stuck up behind the animal's right ear. These modifications improved the transmission range of the equipment to a maximum of 406 m, although the reception of the signal over these distances was unreliable.

For a strong, reliable, signal the receiving equipment had to be placed within 200m of a grazing animal. This was achieved by building a wooden carrier pack that allowed the receiver equipment to be manually transported to within range of the transmitters on the animals (Plate 4.5). A lead-acid battery was used to supply the power when in the field, and added 4 kg to the weight of the receiving equipment. The total weight of the receiving equipment, power supply and carrying pack was 22kg. This load had to be moved when the cattle moved more than 200m away from the receiver.

The data capture and processing program proved to be very unreliable. Overnight data capture was only successful 1 in 4 times, with interrupted power supply leading to failure of the system. An electronic switching device was made so that the power supply could be switched over to a backup-battery after 6 hours of continual use. For overnight data collections power had to be supplied to both the computer and the receivers. The switching device improved the success rate of data capture to 3 out of 4 times.

The data processing module of the program proved less successful than the data capture module. Data from the 4 transmitter channels appeared to get 'mixed up',

with the signal display on the VDU bearing little relation to the animal's actual jaw movement.

The uncovered rubber tube of the resistive transducer was vulnerable to breakage. Frequently the tube broke whilst the transducer was being fitted to the animal, and sometimes the animals returned to the kraal with a broken transducer. When a transducer did survive an observation session, its response to jaw movement diminished with time. A transducer that initially produced a strong signal would only produce a weak response after 3 hours of continual use, due possibly to redistribution of the graphite powder within the silicon rubber.

The telemetric method of monitoring feeding behaviour developed for this project failed to meet any of the design criteria. The system was so unreliable that insufficient data were obtained to enable verification against manual methods of data collection. The transducer was not robust, readily breaking under the stress of normal use and, furthermore, the response of the transducer changed throughout the day and failed to provide any reliable indication of the scale of jaw movement. The labour demand of the system was higher than that of non-automated techniques, requiring at least 2 people to carry the equipment. Results that were obtained were unreliable and, more often than not, could not be synchronised with the observed behaviour of the animal. The equipment had an extremely low success rate, seldom providing complete data.

Despite considerable effort to develop auxiliary transducers to distinguish between biting and chewing movements the telemetric equipment was never able to reliably distinguish between these 2 activities.

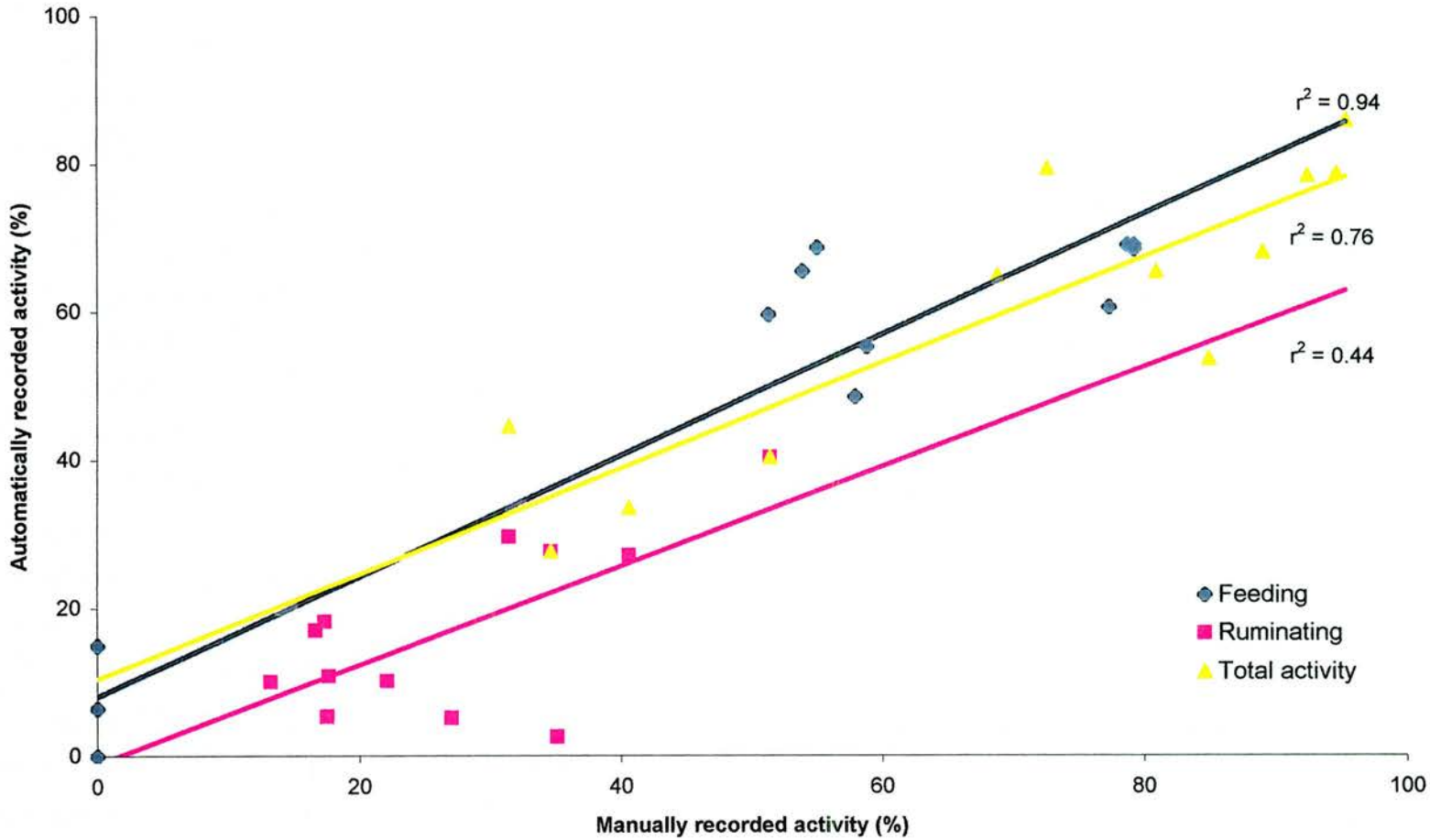
For these reasons, this type of telemetric method is probably unsuitable for use under rangeland conditions. Even if the system tested in this project performed to its specification, allowing a 1km range, its use in the field would still have been difficult without resorting to vehicular transport to carry the equipment. Furthermore, the resistive transducer was not suitable for use under rangeland conditions.

4.3.5: Evaluation of a datalogger method

The Institut National de la Recherche Agronomique (INRA) Portable Electronic Recording Device (IPERD) is a commercially available method of automatically recording feeding behaviour (Plate 4.2, 4.3, and 4.4). It consists of a datalogger, with sufficient memory to store up to 4 days of behavioural data (512 KB), and a pneumatic type of jaw movement transducer. The total weight of the equipment, with batteries, is 350g, the dimensions of the datalogger being 155 x 90 x 45 mm.

The equipment was designed to attach to the back of an animal with connection to the jaw transducer by way of a length of flexible plastic tube. This arrangement was considered unsuitable for use in a rangeland situation because of the risk of the tubing getting caught on trees and bushes. To avoid this happening a halter was designed that included both the datalogger and transducer They were connected by a short length of tube enclosed within the fabric of the halter (Plate 4.4). The IPERD was also modified to allow the datalogger to be switched on and off more easily in the field so reducing the risk of data loss. Once modified, the system provided successful collections 5 times out of 6. However, this success rate was achieved by downloading the IPRED every 12 or 24 hours. Data collection over a 4-day period as recommended by the manufactures never produced a successful result.

Figure 4.2: Manually and automatically recorded feeding, rumination and total feeding activity measured in cattle fitted with a IPRED jaw movement monitor showing correlation coefficients (r^2).



Method

In order to test whether the data collected by the IPERD accurately reflected actual feeding behaviour, twelve 3-hour long observation sessions were conducted with cattle using both automated and manual data collection (scan sampling).

In order to accustom the animals to the IPERD apparatus, a halter containing a dummy datalogger was fitted on the evening before the observation session began. The following morning, the dummy was replaced by the activated IPERD and manual observation of feeding behaviour began the moment the animal was released from the crush. Observations were made every 5 minutes, using the PO to record the data. The focal animal, fitted with the IPERD, was allowed to graze with the main herd. The observers who followed the animals maintained a distance between themselves and the animals of not less than 5 m. In order to collect data when foraging activity was low, on 4 out of the 12 observation sessions animals fitted with IPERD were released into a kraal and not allowed to graze during the 3-hour observation session.

After 3 hours, the animal fitted with the IPERD was returned to the crush, the halter containing the apparatus was removed and the data immediately downloaded onto a PC.

Time spent feeding and ruminating was expressed as a percentage of the total observation time for both manual and automatic observations. Total feeding activity was calculated by the addition of feeding and rumination activity. All data, expressed as percentages, were transformed using arc-sine-root transformations and regression analysis was performed to test how well the 2 sets of observation agreed.

Results

There was a highly significant correlation (r^2 = 0.91, P< 0.001) between feeding activity measured using the 2 methods (Figure 4.2). Mean residual error in the case of feeding activity was ± 8.6 %. The poor spread of data points within the feeding activity data set was a cause for concern. Data points tended to be clustered around the origin, when no feeding activity occurred, or between 50 and 80% activity (Figure 4.2). Regression analysis of the cluster of data points between 50 and 80% activity showed no significant correlation between methods (r^2 =0.21). Regression analysis of the second cluster around the origin was not possible due to the lack of variation in the manually observed data.

Correlation between rumination activity recorded (Figure 4.2) by the 2 methods was significant, but at a lower level than feeding behaviour (r^2=0.44, P<0.05). Further study of the data showed that removal of the 2 data points with poorest fit resulted in a dramatic improvement in the correlation value for rumination activity data (r^2=0.67).

Total feeding activity (Figure 4.2) recorded by the 2 methods showed a highly significant correlation (r^2 = 0.76, P<0.001), with a mean residual error of ±8%. The spread of data points was more even than that of either feeding or rumination activity, with no obvious clustering. Removal of the same 2 poor fitting data points as above increased the correlation coefficient (r^2 =0.86).

Discussion

Removal of the 2 data points with the poorest fit improved the r^2 values for all 3 measured parameters. The poor agreement between methodologies during the observation sessions in which the poor-fitting data points were included could be

explained by poor adjustment of the halter. It was also noticed that biting flies around the face of the animal frequently disrupted the rhythm of rumination bouts, which may have adversely effected the IPERD recognition of rumination patterns and thereby provided spurious data. The poor agreement of methods in the feeding activity cluster between 50and 80% may also be explained by poor adjustment of the halter; rumination activity may have been recorded as feeding activity.

Total activity was more reliably measured than either feeding or rumination activity by IPERD, total activity being measured reliably over a wide range of activity (30 – 95%). The IPERD was, therefore, a better monitor of total oral activity in ruminants than of rumination or feeding activity. Factors such as the adjustment of the halter and the presence of biting flies, reduced the ability of the IPERD to distinguish between rumination and feeding activities.

The labour demand of the IPERD eventually proved to be lower than for manual observation, both during data collection and with data processing. The use of the IPERD in the field had many advantages. However, the success in the current project was only achieved with considerable practice and with major modifications to the original system. A major source of frustration was that once data collection had started there was no indication of how well the equipment was working. It was frequently difficult to trace the cause of data losses or to know exactly how long data had been collected for.

Although the IPERD provided useful behavioural data that showed close agreement to that recorded manually, it could not totally replace manual methods.

4.4: Conclusions

A successful method of recording behavioural data was developed. This method combined flexibility and ease of operation with time-saving features, such as rapid data recording and simultaneous observations. This method was superior to traditional methods because it was easier to operate, more accurate and less time-consuming. The method was used successfully in both Ethiopia and Zimbabwe, when approximately 50,000 individual records were made. Data processing was 'streamlined' using easily edited macros for MSW6 and MSE5. Technical constraints, such as the availability of batteries, was not a serious limitation to its use, even in underdeveloped areas of rural Africa.

The development of automated methods of collecting behavioural data was less successful. The use of telemetric equipment (HORAS) was eventually abandoned because the system proved to be more labour-intensive than non-automated methods of data collection. The quality of data obtained with the telemetric system was greatly inferior to that collected by non-automated means. The use of telemetry was abandoned in favour of dataloggers that have increased memory capacity.

The IPERD method of automated observation was much more successful than HORAS. There was a good correlation between total oral activity recorded with IPERD and that observed by direct observation. Further work is required to improve the adjustment of the harness so that consistent, high-quality data are obtained.

A reliable, automated method of recording feeding behaviour has a valuable role to play in rangeland studies. However, it cannot completely replace direct methods and should not be used as the primary source of behavioural data because data acquired from automated systems represent a machine's interpretation of animal feeding behaviour, often based on oversimplified models of prehension and comminution.

Frequently, machines cannot distinguish between feed-related and non-feed-related oral activity, leading to overestimation of foraging activity. Reliable explanations for overestimation can only be achieved through direct observations.

SECTION 2

FORAGING STRATEGIES OF CATTLE AND DONKEYS IN TRADITIONAL AFRICAN GRAZING SYSTEMS

CHAPTER 5

LITERATURE REVIEW

5.1: Introduction

The effect of restricting feeding (foraging) time (RFT) resulting from traditional African grazing systems (TAGS) on the DMI and foraging behaviour of cattle and donkeys has not been widely studied. The experiments of Romney *et al.* (1996) with goats in Tanzania and of Smith (1961) with cattle in Northern Rhodesia (Zambia) showed that ruminants are able to compensate to some degree for RFT. However, the mechanisms of behavioural compensation strategies (BCS) were not investigated. The capacity of herbivores to compensate for RFT cannot be unlimited and it is likely to be constrained by both forage quality and herbage abundance. Knowledge of BCS will provide a set of indicators by which farmers can judge whether their communally grazed animals are achieving a satisfactory VFI, thereby providing a guide for the provision of strategic supplementation.

The DMI and behavioural response of donkeys to RFT is likely to be different from that of cattle, because equid species are known to spend a longer time grazing than do ruminants (Arnold and Dudzinski, 1978). To date, there have been no reported behavioural studies of donkeys kept under TAGS. Rutagwenda *et al.* (1990) examined the forage preferences of donkeys in Northern Kenya, but no behavioural details were reported. Recently, a few studies concerned with feral or wild asses have been published but these concentrate on social and spatial behaviour, rather than foraging behaviour (Aganga, Tsopita and Seabo, 1994; Canacoo and Avornyo, 1998; Moehlman, Fowler and Roe, 1998; Rudman, 1990). Only Mueller *et al.* (1998) and Blakeway (1994), have studied in detail the foraging behaviour of

donkeys. Both these studies were conducted under temperate conditions. Mueller *et al.* (1998) investigated chewing behaviour in stall-fed donkeys, and Blakeway (1994) studied donkeys grazing rye-grass pastures in Scotland.

The feeding behaviour of ruminants, ponies and horses has been thoroughly investigated, though few of these studies have been comparative. Comparisons between different feeding behaviour studies are made more difficult by the different research questions posed by those who work with ruminants and by those who work with equids. Arnold (1984 a, b) conducted a comparative study using sheep, cattle and horses grazing the same temperate pasture. This study was restricted to measurement of time budgets, circadian activity and the spatial relations of the 3 species and provided little information about possible compensation for RFT.

Investigation of BCS under grazing conditions is difficult due to the limitations of the available techniques for measuring DMI, and the variability in grazing conditions that do not necessarily affect herbivore species in the same way. Therefore, the initial investigation into BCS was carried out with individually penned animals. Under these conditions, the quality of the diet could be controlled and the measurement of nutritional parameters such as DMI, DMD and mean retention time (MRT) could be measured directly with well proven, standard techniques. Furthermore, behavioural observations could be made under controlled conditions when animals were less likely to be disturbed by changes in weather or other environmental conditions.

Subsequent investigations were carried out under rangeland conditions in developing countries (Ethiopia and Zimbabwe), using techniques developed in Section 1 (summarised on pages 60 and 92). In Ethiopia, a study was carried out with cattle to investigate what effect forage supplementation and extended grazing time had on

DMI during 2 seasons of the year. A detailed behavioural study was undertaken to allow BCS of cattle to be studied. In the Zimbabwe study, the effect of grazing access time on DMI and foraging behaviour in both cattle and donkeys was measured during the wet and dry seasons.

Data from these 3 studies provided information about BCS in cattle and donkeys under a broad range of environmental and grazing conditions, resulting in the development of a set of behavioural indicators that farmers could use as a guide for the provision of strategic supplementation.

5.2: Behavioural compensation strategies (BCS)

The behavioural aspects of food intake consist of 3 components: feeding time (FT), bite size (BS) and bite rate (BR) (Stobbs, 1974). Compensation for reduced grazing access time must be achieved by increasing one or more of these components. In the following section, each of these components is discussed in relation to its possible contribution to BCS.

5.2.1: Feeding time (FT)

In ruminants, active FT can be increased by the postponement of other activities, such as rumination and idling, to other periods in the day when no feed is available. Ruminants with limited time to graze tend to postpone rumination until the hours of darkness (Bayer and Waters-Bayer, 1998), allowing more time in the day to be dedicated to foraging. Romney *et al.* (1996) found that goats tethered at grazing for 4 hours per day ruminated for only 0.4% of the available eating time, whilst those tethered at grazing for 8 hours spent 7.2% of the available eating time ruminating. A

similar effect of restricted grazing access on the amount of time spent idling was recorded.

The opportunity to compensate for restricted grazing time by increasing eating time per hour (ETPH) is limited because most of the hours of daylight are already taken up with this activity. Goldson (1963) found that Jersey cattle grazing improved pastures in the Kenyan uplands spent 68% of the daylight hours foraging. Alhassan and Kabuga (1988) working in Ghana with N'dama and Friesian bulls found that the indigenous breed spent 84% of the daylight hours grazing, whilst the exotic breed spent only 72%, possibly due to high ambient day-time temperatures. The work of Smith (1961) showed that the ETPH of cattle given 7-hour access to grazing was only marginally greater (6 minutes per hour) than those given free-access. For donkeys, the possibility of compensating for restricted grazing time by increasing ETPH is limited by their need to complete chewing during the prehensile phase of eating.

A further constraint to increasing ETPH is the quality of the available forage. Both meal length and frequency of meals are determined to some extent by the bulk of the diet (Forbes, 1986). In ruminants, poor quality diets tend to cause an increase in the interval between meals because of the slow rate of passage of food and prolonged gut-distension times (Forbes, 1988). An animal with limited FT may be forced to ruminate or to endure extended periods of idling because of these gut-fill effects.

5.2.2: Bite size (BS)

In ruminants, BS is a major factor that limits intake of grazed forage (Hodgson, 1982a). For an animal of any given size, the weight of each bite is largely determined by the bulk density and canopy structure of the herbage on offer (Ungar, 1996). In cattle, the number of bites per day rarely exceeds 36,000, and to achieve satiety an

adult animal must maintain a BS of more than 0.3 g organic matter (OM) per bite (Stobbs, 1973). Stobbs (1974) measured BS of between 0.05 and 0.50 g OM per bite in adult dairy cattle grazing tropical swards; BS on sparse, open tropical swards was generally less than 0.30 g OM per bite. No similar studies have been carried out with donkeys, although Myers (1994) made some crude measurements of BS in thoroughbred horses and Shetland ponies grazing ryegrass swards. It was found that BS in equids, as in cattle, was constrained by the canopy-structure of the herbage on offer.

Optimal foraging theory would suggest that free-ranging herbivores strive to maximise energy capture per unit of time (Houston, 1993). As intake per bite is the greatest constraint to the rate of energy capture, it is likely that livestock with free access to grazing will endeavour to maximise BS. Consequently, there should be little scope for animals to compensate for loss of eating time by taking bigger bites. This has been verified by Greenwood and Demment (1988) who showed that, although fasted cattle had a higher rate of intake than non-fasted cattle, there was no difference in BS between the 2 groups.

5.2.3: Bite rate (BR)

Whilst BS in a given animal is largely determined by herbage characteristics the factors influencing BR are more complex. The biting process can be simplified assuming a hypothetical system where food is in abundant supply, biting jaw-movements are distinct from chewing jaw-movements and subsequent bites occur as soon as the mouth is clear. In this system, bite rate can be described by the following equation derived from Ungar (1996):

$$Ji = \frac{Jc}{W * Q} \qquad \text{(Equation 5.1)}$$

Where Ji = rate of prehending jaw movements (bites per minute), Jc = rate of chewing jaw movements (chews per minute), W = bite weight (g per bite) and Q = chewing jaw movements per unit mass ingested (chews per g).

Although this simple model does not describe the complex process of prehension accurately, it illustrates some of the major constraints to bite rate in a hungry animal that has free access to palatable food. Use of this model suggests 2 possible mechanisms for compensation for restricted foraging time:

1. For a bite of a given size, bite rate can be increased if chew rates are accelerated, allowing successive bites to be taken more rapidly. Chewing rates are rarely reported for animals at grazing, perhaps due to the difficulty in recording individual chewing jaw movements (Laca *et al.,* 1992). Greenwood and Demment (1988) did, however, record chew rates and showed that fasted cattle chewed more rapidly than non-fasted cattle in the first few hours after being reintroduced to grazing.

2. Bite rate could also be increased by reducing the chewing jaw-movements per unit mass of food ingested, thereby increasing the particle size of swallowed material (Greenwood and Demment, 1988). The consequence of this for ruminants will be an increase in the rate or time spent ruminating. In equids the likely result would be an increase in faecal particle size with probably a decrease in digestibility.

On rangeland where the sward structure is sparse, the bite rate may be constrained by the time taken to select material to eat and an increase in bite rate under these conditions is likely to be achieved at the cost of reduced diet quality. Greenwood and

Demment (1998) failed to show any difference between the NDF content of the diet selected by fasted steers and non-fasted steers grazing Italian ryegrass swards. In contrast, Hatfield *et al.* (1990) showed that on New Mexico rangeland the crude protein content of forage selected by sheep receiving concentrate supplements (and thus presumably closer to satiety and more selective) was higher than for non-supplemented sheep. Evaluation of the effect of night-kraaling on diet selection, based on these 2 studies, is difficult as they involved different species, grazing in different environments with the degree of selection being estimated by different methods.

5.3: Research Objectives

Possible BCS arising from restriction of feeding time may involve all 3 behavioural components of feed intake. However, the 2 most likely mechanisms are by changes in ETPH and/or BR. The response will depend on the quality of the diet on offer and the ease with which it can be prehended and comminuted. Changes in ETPH or BR are likely to affect digestion dynamics, resulting in changes in DMD and MRT.

The hypothesis is that herbivores are able to compensate to some degree for RFT. However, these behavioural responses are limited and are achieved at the expense of diet quality and digestive efficiency. In order to investigate this hypothesis the objectives of the following 3 chapters are:

1. to investigate and compare the behavioural response of cattle and donkeys to RFT and to identify BCS;
2. to identify changes in gut dynamics resulting from RFT that may lead to changes in DMD and MRT in cattle and donkeys;

3. to examine BCS in cattle and donkeys in response to seasonal changes in grazing conditions;
4. to identify behavioural factors that may indicate when RFT is limiting nutrient intake in cattle and donkeys.

CHAPTER 6

PRELIMINARY INVESTIGATION OF THE FORAGING STRATEGIES OF CATTLE, PONIES AND DONKEYS UNDER CONTROLLED EXPERIMENTAL CONDITIONS

6.1: Introduction

The available methods for measuring nutritional and behavioural parameters at grazing are far from ideal and lack precision (see Chapter 2). Research into BCS requires the precise measurement of DMI, DMD and MRT under environmental conditions that do not influence ingestive behaviour.

Only a few studies have investigated the effect of RFT on feed intake and most of these have been in the context of the effect of work on DMI, and RFT has been incidental to the main thrust of the work. Seldom however, have these experiments reduced feeding time to the level whereby there has been an effect on DMI. Pearson and Smith (1994) showed an effect on DMI in cattle and buffalo fed barley straw when feeding time was restricted to 17 hours. Nengomasha (1997) restricted the feeding time of donkeys fed poor quality bush hay to 19 hours per day and found no effect on DMI. The current experiment was designed to constrain DMI by limiting feed access to 8 hours per 24 hours.

Little research work into the nutrition of donkeys has been reported, and still fewer papers have been published about donkey feeding behaviour. However, the nutrition and feeding behaviour of the horse is relatively well researched. For this reason, native ponies were included in the investigation to act as a 'bench mark' against which results could be compared with published data.

The response of animals to RFT is likely to depend on the nature of the diet offered. Diets with high levels of indigestible fibre are likely to have lower DMI and rates of

intake than diets with lower levels of indigestible fibre. The under noted experiment used alfalfa, haylage and straw so that the effect of feed type on RFT could be investigated.

6.2: Materials and methods

6.2.1: Animals and management

The experiment was carried out at the CTVM, Edinburgh in the summer of 1994. Four 1-year old, castrate male cattle, mean live weight at the start of the experiment 230 kg (s.e. ±5.5), 4 mature castrate donkeys, mean live weight at the start of the experiment 199 kg (s.e. ±6.6) and 4 mature castrate ponies mean live weight at the start of the experiment 210 kg (s.e. ±6.1) were used.

The animals were housed in a large open barn and penned in groups of 4 according to species. During the adaptation and collection phases for each treatment, animals were tethered separately to ensure there was no cross-feeding between troughs and to facilitate individual faecal collection. Rubber mats were provided to allow the animals to lie down in comfort. A rest period was provided between each treatment period, when the animals were allowed to graze.

Food was offered in excess (+15% of the previous day's fresh intake) to each animal during the hours when food was available and there was free access to water at all times. All animals were given 14 days to adapt to each of the diets and the environmental conditions. Data were collected during the following fourteen days of each experimental period.

The amount of feeding time was restricted to 8 hours per day as this is the typical amount of time spent grazing by cattle and donkeys under TAGS (Bayer and

Waters-Bayer, 1998). Feeding time was restricted by fasting the animals overnight from 17:00 in the evening to 09:00 h the following morning, providing a feed access time of 8 hours during daylight hours.

6.2.2: Diets

The diets consisted of 3 different quality fibre feeds:

(i) A high quality diet of finely-chopped (2 cm) alfalfa, with a high potential ingestion rate and short MRT.

(ii) A medium quality diet of long, high-dry-matter haylage (70% DM), with moderate potential ingestion rate and MRT.

(iii) A poor quality diet of barley straw, with a low potential ingestion rate and long MRT.

During each experimental period all animals received the same diet. The sequence of treatments is shown in Table 6.1. The mean composition of the diets is shown in Table 6.2.

Table 6.1. Sequence of diet treatments, showing faecal collection (FC) and any behavioural observation (BO) periods

Week no.	1-2	3	4	5	6-7	8	9	10	11-12	13	14
Diet	Haylage				Alfalfa				Straw		
Activity	Adaptation	Data collection		Rest	Adaptation	Data collection		Rest	Adaptation	Data collection	
Procedure		FC	BO			FC	BO			FC	BO

Table 6.2. Mean chemical composition (g/kg DM unless shown) (± s.e) of the diets offered (n = 12)

	Haylage	Alfalfa	Barley Straw
Dry matter (g/kg)	683.0 (6.34)	892.0 (8.51)	826.0 (2.83)
Organic matter	935.5 (6.27)	884.9 (2.54)	960.4 (1.42)
Neutral-detergent fibre	655.5 (12.91)	381.94 (7.84)	824.0 (8.31)
Acid-detergent fibre	392.0 (20.80)	288.7 (13.58)	529.0 (14.53)
Crude protein	97.6 (4.94)	197.9 (4.01)	27.6 (1.11)
Gross energy (MJ/kg DM)	19.5 (0.34)	16.1 (0.44)	19.0 (0.12)

6.2.3: Measurements

Live weight

All animals were weighed twice weekly to monitor changes in live weight.

Dry matter intake

Every morning, food for an individual animal was weighed into a large bin. Approximately half the food in the bin was placed before the animal at 09:00 h, and the feeding trough was topped up periodically during the day as the quantity of food diminished. A ~100 g representative sample of the food offered was taken for dry matter analysis and another 50 g sample was added to a weekly, pooled sample of the food offered for subsequent proximate analysis.

At 17:00 h each day, the food that had not been eaten was removed, weighed, mixed and a representative sample taken for dry matter analysis and a smaller sample added to a pooled weekly sample of refused food for subsequent proximate analysis. Any

food that had fallen on the floor was picked-up, weighed, mixed and a representative sample taken for dry matter analysis.

Daily DMI for each animal was calculated by subtracting the amount of dry food refused (both bin and floor refusals) from the amount of dry food offered.

Faecal output and mean retention time

A 7-day total faecal collection was carried out during each of the 3 treatment periods. Immediately before the collection period began all faeces lying on the floor were collected and discarded and the floor thoroughly swept and washed. At 0:00 h the floor was checked for the absence of faeces and each animal was dosed with 50 g of chromium-mordanted fibre.

At 8:00 h the next morning all faeces produced since dosing were collected and placed in a large bin and the weight of fresh faeces was recorded. The faeces were thoroughly mixed and a 200-300g sample taken. This process was repeated at pre-set intervals during the 7-day collection period (see Table 6.3 for the collection schedule.

The DM content of 150-200g of each sample collected was determined by drying in a force-draught oven at 100°C and retained for subsequent chromium analysis. In addition, a sub-sample representing 3 percent of the fresh weight of faeces produced during the collection period was taken. The sub-sample was frozen, and at a later date, pooled with all the other 3 percent samples gathered from each animal during that particular collection period. After thawing, the pooled sub-samples were thoroughly mixed and a 300g representative sample removed, dried at 65°C until constant weight and retained for analysis.

Table 6.3: Faecal sampling schedule for the mean retention time (MRT) study

Collection day	Sampling time						
1	08:00 h	10:00 h	12:00 h	14:00h	16:00h	19:00h	22:00
2	06:00 h	08:00h	10:00h	12:00 h	14:00 h	16:00 h	19:00h
3	06:00 h	09:00 h	12:00 h	16:00 h	18:00 h		
4	08:00 h	12:00 h	16:00 h	19:00 h			
5	08:00 h	18:00 h					
6	08:00 h	18:00 h					
7	08:00 h	18:00 h					

Composition of diets

Feed and faecal samples kept for analysis were analysed for organic matter, neutral detergent fibre, acid detergent fibre, crude protein and gross energy according to the methods of the Association of Official Analytical Chemists (1990).

Digestibility

The apparent DMD of roughage was calculated from the mean DMI and mean dry FO over the 7-day faecal collection period, using the equation:

$$DMD = 1 - \left(\frac{FO}{DMI} \right) \qquad \text{(Equation 6.1)}$$

Degree of selection

When alfalfa was fed, the fraction of stem in the refused food from all animals was determined by passing 100g of a dried sample through a 2 mm sieve. A sample of the

food offered was treated similarly. The difference in the leaf:stem ratio of food offered and food refused was calculated.

It was not possible to carry out a similar analysis during the haylage and straw treatments because of the length of the feed material. Furthermore, selection was not apparent with these diets.

6.2.4: Behavioral observations

In order to reduce disturbance to the animals to a minimum during behavioural data collection, observations were carried out for a 5-day period in the week following the digestibility trial.

Scan observations

During working hours (08:00 - 17:00h) the animals were observed and behavioural data were collected using a scan-sampling technique. This involved recording the behaviour of each animal every 5 minutes over a 3-hour observation session (Hodgson, 1982b). The day was divided into three, 3-hour observation sessions starting at 08:00h, 11:00h and 14:00h. Each 3-hour session was replicated 3 times during the 5-day period. A maximum of 2 observation sessions were carried out per day, and the same observer made all observations.

During each 3-hour observation session, 36 observations were made for each animal. These data were recorded by entering codes on a grid-sheet. Two categories of behaviour (position and oral activity) were recorded, each of which was assigned a line in the grid. Each individual activity within a category was assigned a code as described in Table 6.4.

Table 6.4: Codes assigned to various activities within each behavioural category.

Category	Activity	Code
Position	Standing (still)	1
	Standing (moving)	2
	Lying down	3
	Other	4
Oral	Eating	1
	Ruminating	2
	Other	3

During non-working hours (17:00 h - 08:00 h) a time-lapse video was used to record the activity of the animals. The video was set to record at 5 frames per second. These videos were later analysed using the same recording sheets that had been used for the direct observations. A time reference was recorded on the videotape, allowing it to be fast-forwarded in 5-minute increments so that observations were recorded in a way similar to the daylight records. Three replicates of each of the night observation sessions were made.

For both the direct observations and those recorded on videotape, the number of times a particular activity was observed during all 3 replicates was summed for each hour of observation. For each observation hour, the total number of times each activity was observed was expressed as the mean number of minutes per hour spent in that activity, in order to create a composite circadian behaviour pattern for each activity. By summing the mean number of minutes per hour spent in each activity over 24 hours, the total amount of time per day could be calculated.

Focal observations

Focal observations were carried out twice a day, firstly in the hour immediately after food was given and secondly in the hour immediately prior to the withdrawal of food. These observations were carried out by 3 different observers on each of the 5 days of the behaviour study.

Each animal was observed for 5 minutes, during which time repeated measurements of the amount of time (in seconds) taken for 20 mouth movements were recorded. As many measurements as possible within the 5-minute observation time were taken. The 20 mouth movements included bites and chews. To allow both bite rates and chew rates to be calculated, the number of mouth movements that were bites was also recorded. If cattle happened to be ruminating during the observation time, the amount of time for 20 cud chews was measured and recorded in a different column.

Bite rate (bites per minute) was calculated using the following formula:

$$\text{Bite rate} = \frac{\text{number of bites in 20 mouth movements}}{\text{time taken for 20 mouth movements}} \times 60 \quad \text{(Equation 6.2)}$$

Chew rate (chews per minute) was calculated using the following formula:

$$\text{Chew rate} = \frac{20 - (\text{number of bites in 20 mouth movements})}{\text{time taken for 20 mouth movements}} \times 60 \quad \text{(Equation 6.3)}$$

The sequence in which animals were observed was rotated to prevent the effect of time-since-feeding confounding the scan data, as satiety probably had an effect on oral activity.

6.2.5: Statistical analysis

Analysis of variance (ANOVA) was carried out using Minitab (version 8.2). Data were first checked for normality and equality of variance using Minitab's N-score method and an *F*-distribution test prior to full analysis.

Where parameters were expressed as proportions, statistical analysis was performed on arc-sine transformed data (Martin and Bateson, 1996).

6.3: Results

All animals remained in good health during the course of the experiment, and all experimental treatments were completed as planned.

Techniques

The night-time observations of rumination behaviour in the cattle using time-lapse video equipment proved problematic and did not provide satisfactory data. The frame speed of 5 per second did not allow individual jaw movements to be recorded and, therefore, body posture and bolus-swallowing had to be relied on to identify rumination. Furthermore, the use of a single camera to simultaneously record the behaviour of 4 animals was not successful, as the animals heads were frequently obscured. Although the rumination observations are presented in Table 6.9, the reliability of the data is questionable. The reliability of the bite rate data was also doubtful, as there were large differences in bite rates recorded by different observers.

Live weight changes

There was a significant increase ($P<0.01$) in the live weight of cattle over the course of the experiment and a significant difference between the second (alfalfa) and third (straw) treatment periods. The difference in live weight between the first (haylage)

and second (alfalfa) treatment was significant ($P<0.05$). In donkeys, there was a highly significant ($P<0.01$) decrease in live weight between the second (alfalfa) and third (straw) treatment. There was no significant change in the live weight of ponies over the whole experiment (Table 6.5).

The large difference in changes in live weight between cattle and the 2 equid species reflected the difference in the degree of maturity between the 2 types of herbivore. The donkeys and ponies had achieved maturity, whereas the cattle were still growing. Animals of similar live weight, but differing in maturity, were selected for the experiment because the effect of body size was considered to have a greater effect on the rate of intake than the effect of maturity.

The only significant changes in live weight (Table 6.5) during the treatments occurred with cattle during the alfalfa treatment ($P< 0.05$) and donkeys during the straw treatment ($P<0.05$). The immature cattle maintained some growth during both haylage and alfalfa treatments (1.8 and 11.7 kg respectively), but lost weight during the straw treatment (0.8 kg).

Table 6.5: Mean (±s.e.) live weight and live-weight changes of cattle, donkeys and ponies fed haylage, alfalfa or barley straw

	Cattle	Donkeys	Ponies
	Live weight (kg)		
Haylage	230 (9.3)[a,b]	199 (6.6)[e]	210 (6.1)
Alfalfa	246 (7.5)[a,c]	200 (6.4)[d]	206 (5.5)
Straw	295 (14.0)[b,c]	183 (8.4)[d,e]	212 (3.7)
	Change in live weight during each treatment (kg/28 days)		
Haylage	1.8 (2.2)[*]	-1.7 (0.7)	-2.2 (1.3)
Alfalfa	11.7 (2.4)	0.0 (1.1)	-1.4 (0.9)
Straw	-0.8 (4.9)	2.5 (0.7)[d]	-5.8 (3.0)

[a] values with the same superscript differ significantly ($P < 0.05$).

[b,c,d,e] values with the same superscript differ significantly ($P < 0.01$).

[*] live weight change was significant over the course of the treatment ($P<0.05$).

Dry matter intake

Cattle ate significantly more food per unit of metabolic weight than did donkeys ($P<0.01$) and ponies ($P<0.05$); there was no significant difference in intake between ponies and donkeys. Cattle ate significantly more during the alfalfa treatment than during either haylage ($P<0.01$) or straw treatments ($P<0.001$), and ate significantly more haylage than straw ($P<0.05$). Donkeys ate significantly less straw than alfalfa or haylage ($P<0.05$); there were no significant differences between straw and alfalfa intake (Table 6.6). In ponies, there was a significant difference only in intakes between the alfalfa and straw treatments ($P<0.01$) (Table 6.6).

During the alfalfa and haylage treatment, there were significant differences in dry matter intake per unit of metabolic weight between cattle and the 2 equid species (Table 6.6). There were no significant differences between cattle, donkeys and ponies in intake per unit of metabolic weight during the straw treatment

Table 6.6: Mean (± s.e.) dry matter intake per day and per unit of metabolic live weight in cattle, donkeys and ponies fed haylage, alfalfa or barley straw.

	Cattle	Donkeys	Ponies
Dry matter intake (kg per day)			
Haylage	4.4 (0.22)[a,c]	3.2 (0.21)[d]	3.4 (0.26)
Alfalfa	6.5 (0.35)[a,b]	3.6 (0.23)[e]	4.2 (0.24)[f]
Straw	3.9 (0.28)[b,c]	2.3 (0.40)[d,e]	2.6 (0.10)[f]
Dry Matter Intake per unit metabolic weight (g/kg $M^{0.75}$)			
Haylage	74.7 (2.7)[g,h]	60.3 (2.6)[g]	60.6 (4.5)[h]
Alfalfa	104.4 (3.5)[i,j]	66.9 (2.8)[i]	77.7 (3.8)[j]
Straw	54.7 (2.6)	46.2 (6.5)	46.9 (1.4)

c,d,e,g,h values with the same superscript differ significantly ($P < 0.05$).
a,f,j values with the same superscript differ significantly ($P < 0.01$).
b,i values with the same superscript differ significantly ($P < 0.001$).

Digestibility

Overall, alfalfa was significantly more digestible than the other 2 diets ($P<0.001$), and haylage was more digestible than straw ($P<0.05$) (Table 6.7).

The only significant difference between digestibility of straw and haylage was in ponies ($P<0.05$). Although not significant, haylage was also consistently more digestible than straw in both cattle and donkeys (Table 6.7).

The only significant difference in digestibility between species occurred with the straw treatment. Cattle and donkeys were able to digest straw significantly ($P < 0.05$) better than the ponies. Ranking of the digestibility of each diet by species, showed that whilst ponies were more efficient than cattle at digesting alfalfa, the reverse was true during haylage and straw treatments. The digestibility values for

alfalfa and haylage diets consumed by donkeys were between those of cattle and ponies, whilst there was very little difference between cattle and donkeys in digesting straw (Table 6.7)

Table 6.7: Mean (± s.e.) dry matter digestibility in cattle, donkeys and ponies fed haylage, alfalfa or barley straw

	Cattle	Donkeys	Ponies
Haylage	0.57 (0.022)[a]	0.54 (0.025)[c]	0.52 (0.011)[g,e]
Alfalfa	0.72 (0.013)[a,b]	0.73 (0.016)[c,d]	0.75 (0.011)[e,f]
Straw	0.52 (0.034)[b,h]	0.53 (0.023)[d,i]	0.44 (0.021)[g,f,h,i]

g,h,i values with the same superscript differ significantly ($P < 0.05$).
a values with the same superscript differ significantly ($P < 0.01$).
b,c,d,e,f values with the same superscript differ significantly ($P < 0.001$).

Mean particle retention time

Mean particle retention times are shown in Table 6.8. There were no significant differences between species in MRT, and no significant interactions between species and diet. Furthermore, there were no significant differences in MRT between haylage and straw diets. However, MRT of alfalfa was significantly shorter than those of the other 2 diets ($P<0.001$) for all species.

Table 6.8: Mean (± s.e.) particle retention time (hours) in cattle, donkeys and ponies fed haylage, alfalfa or barley straw.

	Cattle	Donkeys	Ponies
Haylage	47.0 (1.02)	51.8 (0.74)	48.8 (1.91)
Alfalfa	37.6 (1.85)	40.8 (1.83)	43.2 (2.92)
Straw	54.8 (4.03)	53.3 (2.84)	50.6 (2.03)

Degree of selection

During the alfalfa treatment, donkeys, ponies and cattle all selected diets significantly different in stem content compared to the diet on offer ($P<0.01$, $P<0.05$ and $P<0.05$, respectively). Donkeys showed the greatest degree of selectivity, consuming a diet that had, on average, 20% more stem than the feed on offer. Ponies were almost as selective, consuming a diet 18% higher in stem content. Cattle were the least selective, consuming a diet containing only 8% more stem than the food on offer.

Behavioural observations

Time budgets

Time spent eating and ruminating is shown in Table 6.9. Although DMI was highest in all animals when fed alfalfa, time spent eating was significantly less than when fed either haylage ($P < 0.001$) or straw ($P<0.01$). There were no significant differences in the time spent eating between the straw and haylage treatments. Across all the diets ponies spent significantly more time eating than either cattle or donkeys ($P <0.001$).

Cattle spent significantly more time ruminating during haylage treatment than during the other 2 treatments ($P<0.001$). There was no significant difference in time spent ruminating when fed either alfalfa or straw. These results should be interpreted with caution due to the unreliability of the time-lapse video recordings.

Table 6.9: Mean time spent eating per day (±s.e.), amount of available eating time spent eating (%), mean time spent ruminating (±s.e.) and number of observations in cattle, donkeys and ponies fed haylage, alfalfa or barley straw

	Cattle	Donkeys	Ponies
	Time spent eating (minutes per day)		
Haylage	371 (10.2)[a]	374 (14.5)[c]	393 (11.2)[e]
Alfalfa	204 (20.3)[a,b]	261 (20.3)[c,d]	317 (22.1)[e,f]
Straw	414 (11.6)[b]	363 (22.7)[d]	423 (10.6)[f]
	Amount of available eating time spent eating (%)		
Haylage	77 (2.1)	78 (2.9)	82 (2.3)
Alfalfa	43 (4.2)	54 (4.1)	66 (4.6)
Straw	86 (2.3)	76 (4.6)	88 (2.1)
	Time spent ruminating (minutes)		
Haylage	517 (20.7)[g,h]	-	-
Alfalfa	339 (47.2)[g]	-	-
Straw	372 (20.5)[h]	-	-
	Number of observations		
Haylage	1992	1276	1280
Alfalfa	2060	978	978
Straw	2229	1078	1079

[f] values that share the same superscript differ significantly ($P < 0.01$).

[a,b,c,d,e,g,h] values that share the same superscript differ significantly ($P < 0.001$).

During the alfalfa and straw treatments, little rumination occurred during the times that animals had access to feed. However, during the haylage treatment approximately 60 minutes of the available feeding time was spent ruminating, with much (30 minutes) of this activity occurring between 14:00 h and 15:00h.

Focal studies

Bite and chew counts were used to calculate rate of intake, bite size, chews per unit dry mass ingested and rumination rates per unit dry mass. Data is presented in Table 6.10.

Table 6.10: Mean bite and chew rates (±s.e.) during morning (AM) and afternoon (PM) observation sessions of cattle, donkeys and ponies, fed haylage, alfalfa or barley straw.

	Cattle	Donkeys	Ponies
	Bite rate (bites per minute)		
Haylage			
AM	8.4 (0.41)	6.4 (0.92)	8.3 (0.32)
PM	6.1 (0.88)	4.5 (0.61)	6.7 (0.15)
Alfalfa			
AM	4.0 (0.23)	4.7 (0.39)	5.8 (0.52)
PM	3.3 (0.27)	2.9 (0.11)	4.4 (0.44)
Straw			
AM	8.8 (0.71)	6.0 (1.04)	8.2 (0.51)
PM	6.0 (0.80)	5.0 (0.62)	6.8 (0.63)
	Chew rate (chews per minute)		
Haylage			
AM	62.7 (1.21)	51.3 (2.42)	62.5 (1.36)
PM	71.8 (2.63)	51.6 (3.31)	58.5 (5.17)
Alfalfa			
AM	61.2 (2.07)	59.2 (1.51)	57.2 (1.78)
PM	50.2 (2.88)	46.8 (2.01)	44.1 (1.43)
Straw			
AM	62.7 (1.21)	51.3 (2.43)	62.5 (1.32)
PM	71.8 (2.62)	51.6 (3.38)	58.5 (5.14)

Rate of intake

Statistical analysis of intake rates (mg DM/min/$M^{0.75}$) (Table 6.11) showed that the alfalfa diet was consumed at a significantly higher rate than the other 2 diets ($P<0.001$). Overall, there were no significant differences between the rates of intake of straw and haylage. Cattle were able to consume food at a significantly greater rate relative to metabolic weight than either donkeys ($P< 0.01$) or ponies ($P<0.001$) regardless of diet. There were no significant differences between the intake rates of donkeys and ponies.

Eating time per hour

In all 3 species, eating time per hour (ETPH) was highest in the first hour after the reintroduction of food and declined steadily throughout the day. During the alfalfa treatment, ETPH of cattle declined rapidly from the start of the second hour after food was reintroduced. In donkeys and ponies the decline in ETPH throughout the day was slower than in cattle.

When fed straw, ETPH was maintained at a high level throughout the day by all 3 species, never falling below 40 minutes per hour. In ponies, ETPH during the straw treatment did not fall below 50 minutes per hour until an hour before food was withdrawn.

Table 6.11: Mean intake rates, bite size and rumination rates per unit of metabolic live weight (±s.e.) of cattle, donkeys and ponies, fed haylage, alfalfa or barley straw.

Species	Cattle	Donkeys	Ponies
	Rate of DMI per $M^{0.75}$ (mg DM/minute/$kg^{0.75}$)		
Haylage	201 (10.6)[a]	163 (11.3)	156 (15.5)
Alfalfa	531 (69.5)[a,b]	259 (19.3)[c]	250 (27.5)[d]
Straw	133 (9.3)[b]	126 (12.4)[c]	111 (4.6)[d]
	Bite size per $M^{0.75}$ (mg DM/bite/$kg^{0.75}$)		
Haylage	28 (3.0)	30 (2.2)	21 (2.4)
Alfalfa	147 (21.2)	69 (8.5)	49 (4.1)
Straw	19 (2.5)	23 (2.6)	15 (1.2)
	Chews per unit mass ingested (Chews/g DM)		
Haylage	5.7 (0.01)	6.0 (0.19)	7.0 (0.13)
Alfalfa	1.8 (0.14)	3.8 (0.15)	3.8 (0.14)
Straw	7.1 (0.08)	8.1 (0.16)	9.8 (0.32)
	Rumination rate per $M^{0.75}$ (mg DM/minute/$kg^{0.75}$)		
Haylage	145 (6.3)		
Alfalfa	286 (52.4)		
Straw	148 (5.3)		

[c,d] values that share the same superscript differ significantly ($P < 0.01$).

[a,b] values that share the same superscript differ significantly ($P < 0.001$).

Figure 6.1: Time spent eating (minutes per hour) by cattle given 8 hours access to alfalfa, haylage or barley straw

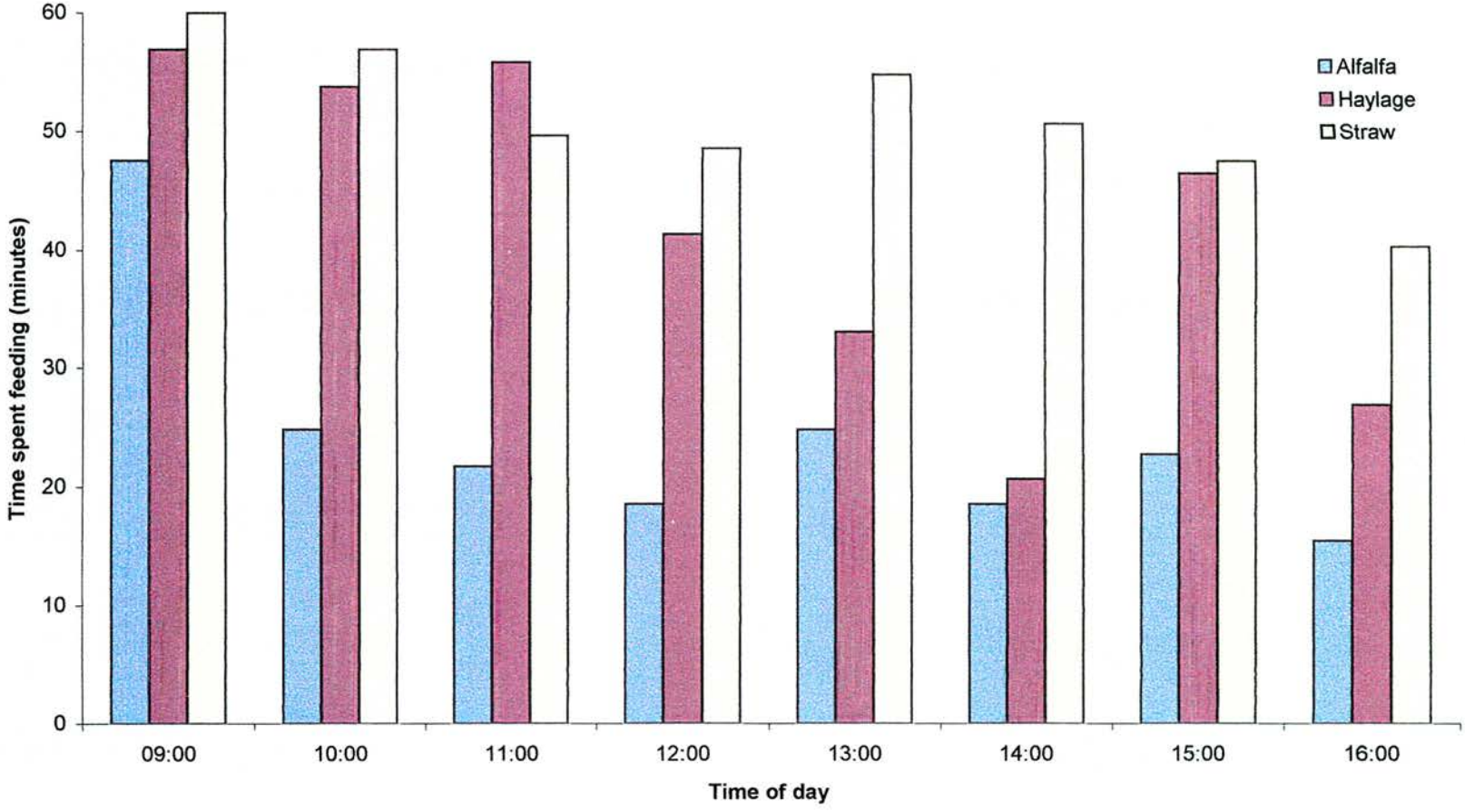


Figure 6.2: Time spent eating (minutes per hour) by donkeys given 8 hours access to alfalfa, haylage or barley straw

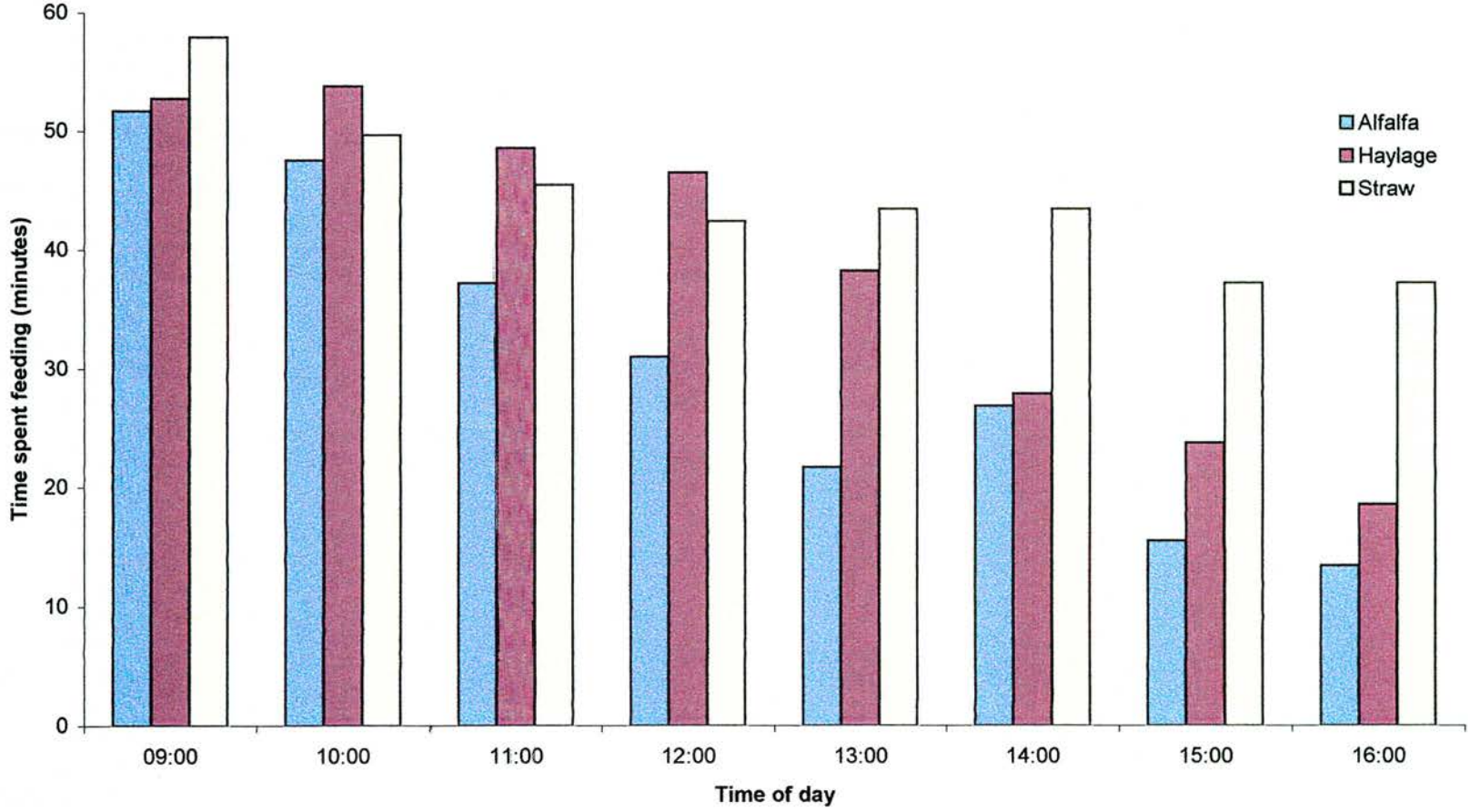
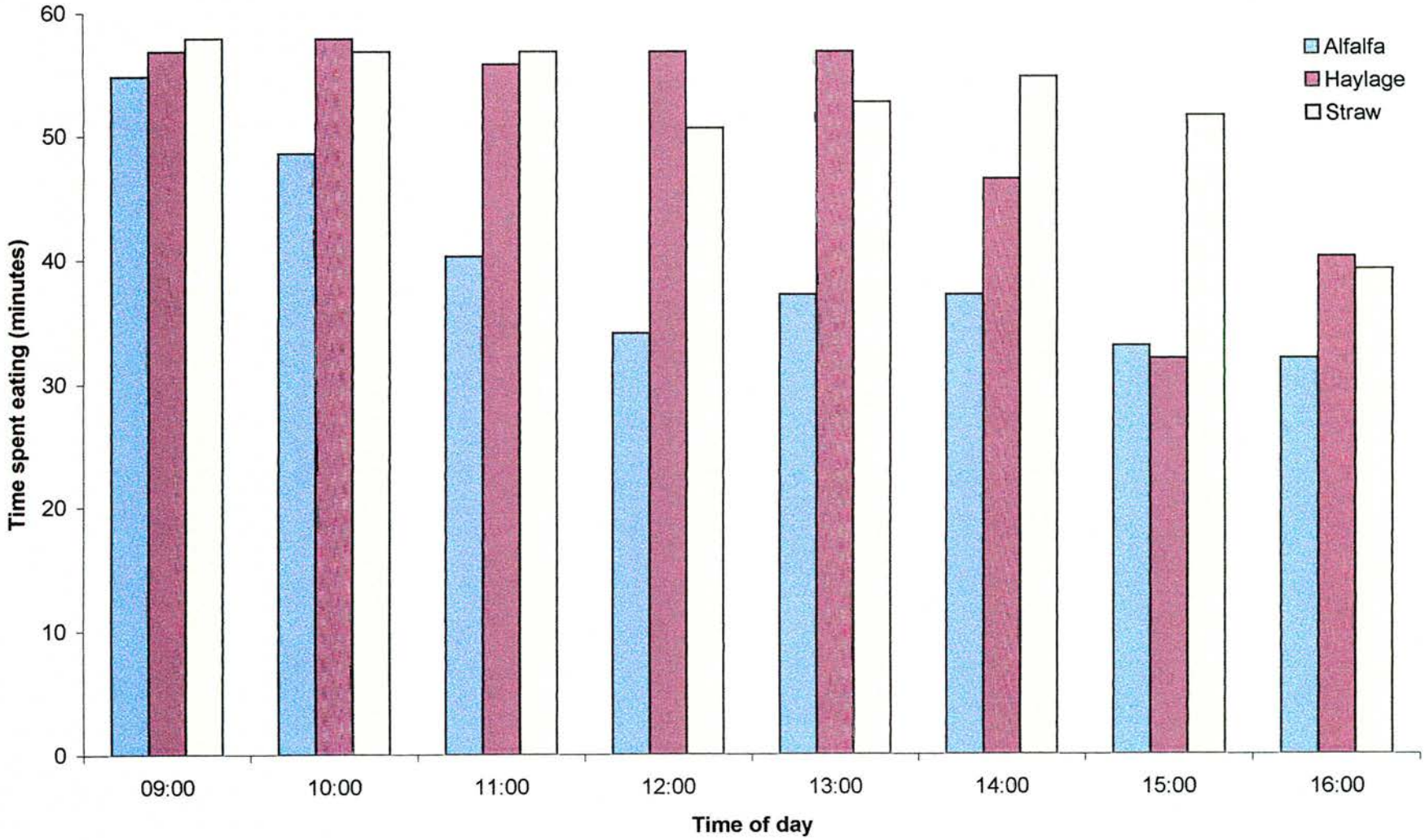


Figure 6.3: Time spent eating (minutes per hour) in ponies given 8 hours access to alfalfa, haylage or barley



6.4: Discussion

6.4.1: Effect of time of access to feed on dry matter intake

Alfalfa

When cattle were fed alfalfa there was little effect of restricted food access on DMI, since mean DMI (104.4 g per kg $M^{0.75}$) was higher than that predicted by both the ARC (1980) model for ruminants fed forage diets (85.8 g per kg $M^{0.75}$) and the Ministry of Agriculture Food and Fisheries (MAFF) (1987) model for lactating cattle (99.2 g per kg $M^{0.75}$). Further evidence for this was provided by the live weight data. The live-weight gain per day (LWG) of cattle fed alfalfa was in excess of that predicted by the MAFF (1987) model (predicted LWG=0.57 kg), suggesting that limited access to food was not reducing growth rate.

Pearson and Cuddeford (unpublished data) recorded a DMI of 129.87 g per kg $M^{0.75}$ in Hereford x Friesian cattle of 450 kg live weight fed *ad libitum* with an alfalfa diet similar to that used in the present experiment. Levels of intake of this order are in excess of those predicted by models for lactating dairy cows fed high-quality forages (MAFF, 1987). The very high DMI of chopped and dried alfalfa measured in the present experiment, and by Pearson and Cuddeford (unpublished data), may be explained by the friability of alfalfa leaf, which readily fragmented into very small particles. These particles would be expected to have a high rate of passage resulting in lower DMD and higher VFI (Minson, 1982). This may explain why, during the present experiment, cattle fed alfalfa had a shorter MRT and lower DMD than had the 2 equid species, and why DMI of cattle was not constrained by gut fill when fed this diet.

The DMI of alfalfa by donkeys (66.9 g per kg $M^{0.75}$) and ponies (77.7 g per kg $M^{0.75}$) was much lower than that measured by Pearson, Archibald and Muirhead (1998), who fed alfalfa *ad libitum* to donkeys (DMI 100 g per kg $M^{0.75}$) and ponies (DMI 155 g per kg $M^{0.75}$). The DMI of ponies and donkeys was less than the 2.5% of live weight suggested by NRC (1989) nutrient requirement tables although there was no significant change in live weight in either of the equids. Pearson *et al.* (1998) showed that donkeys and ponies, with *ad libitum* access to alfalfa, did not regulate their DMI in accordance with their energy requirement and tended to gain weight. Comparison of published results with the results from the present experiment indicate that the DMI of alfalfa in both equid species was constrained by RFT.

Haylage

When cattle were fed haylage, DMI (74.7 g per kg $M^{0.75}$) was close to that predicted by the ARC (1980) model (73.0 g per kg $M^{0.75}$) and to that measured by Pearson and Cuddeford (unpublished data) in cattle fed *ad libitum* hay (73.59 g per kg $M^{0.75}$). Growth rates during haylage treatment were similar to those predicted by the MAFF (1987) model, indicating that restricted food access was not limiting DMI.

The DMI of haylage by donkeys (60.3 g per kg $M^{0.75}$) and ponies (60.6 g per kg $M^{0.75}$) was lower than that measured by Pearson and Merritt (1991) in donkeys (80.9 g per kg $M^{0.75}$) and ponies (99.1 g per kg $M^{0.75}$) fed medium-quality hay *ad libitum*. It was also lower than the DMI recorded by Pearson and Cuddeford (unpublished data) in donkeys and ponies fed 2 hays of medium and low quality *ad libitum*. As the live weight of both equid species also declined when fed haylage, indications are that DMI was limited by RFT.

Straw

The DMI of straw by cattle (54.7 g per kg $M^{0.75}$) was slightly lower than that predicted by the ARC (1980) model (64.5 g per kg $M^{0.75}$) and considerably lower than that recorded by Pearson and Smith (1994) in adult cattle with 20-hour (83.2 g per kg $M^{0.75}$) or 17-hour (75.1 per kg $M^{0.75}$) access to barley straw. Weight loss of cattle fed straw was greater than predicted by the MAFF (1987) model (LWG=-0.04 kg), suggesting that feed access was limiting DMI, resulting in greater weight losses than would have occurred if the animals had 24-hour access to straw.

The DMI of straw by donkeys (46.2 g per kg $M^{0.75}$) and ponies (46.9 g per kg $M^{0.75}$) was lower than that measured by Pearson *et al.* (1998) in donkeys (54.9 g per kg $M^{0.75}$) and ponies (94.7 g per kg $M^{0.75}$) fed a chopped, oat straw diet *ad libitum.* The DMI of donkeys and ponies was also lower than that recorded by Cuddeford *et al.* (1995) in donkeys (56.1 g per kg $M^{0.75}$), Highland ponies (52.3 g per kg $M^{0.75}$) and Shetland ponies (49.0 g per kg $M^{0.75}$) fed chopped, molassed, oat straw *ad libitum.* Values obtained for DMI of straw-fed donkeys in the present study were, however, higher than that measured by Pearson and Merritt (1991) in donkeys fed barley straw *ad libitum* (36.8 g per kg $M^{0.75}$); ponies fed the same diet achieved a DMI (59.8 g per kg $M^{0.75}$) greater than was measured in the present study.

Whilst ponies fed straw lost an average of 5.8 kg live weight over a 4-week period, donkeys fed the same diet gained on average 2.5 kg live weight. The increase in the live weight of donkeys was probably a result of gut fill, possibly as a result of prolonged MRT.

Overall, restricting the time of access to feed had a greater effect on the DMI of ponies and donkeys than on cattle. This was due to equids having slower rates of

intake and smaller bite sizes than cattle. Slower food intake by equids resulted from the need for these species to complete comminution before swallowing. In cattle, comminution would be completed during rumination.

6.4.2: Comparison of the feeding behaviour of cattle, donkeys and ponies

The results from this experiment indicated that the feeding behaviour of donkeys was different from that of both cattle and ponies. Donkeys had a larger bite size relative to body weight than ponies (and, in most cases, cattle) and spent less time eating than ponies. In spite of these behavioural adaptations to attain high rates of DMI, donkeys still demonstrated a greater degree of feed selection during alfalfa treatment than either ponies or cattle.

Donkeys and ponies selected stem in preference to leaf material when fed alfalfa. Whilst these findings support the theory of Janis (1976), who suggested that, in evolutionary terms, the equid species developed a feeding strategy of selecting more fibrous herbage, they contradict optimal foraging theory. This states that, 'animals maximise net energy capture per unit of time' (Houston, 1993). Selection of stem material from the alfalfa diet may have been motivated by taste combined with anatomical adaptations which facilitate greater selection; the morphology of the jaw and mobility of the lips allowing equids to be more highly selective feeders than cattle (Arnold and Dudzinski, 1978). Alfalfa leaf contains high levels of bitter-tasting saponins (Msiska, 1986; D'Mello, 1982) and rats and pigs have been shown to select against diets with high saponin contents (Cheeke, Pedersen and England, 1978).

This difference in feeding behaviour between ruminants and equids may be explained by evolutionary differences in the predator-defence strategies adopted by

the 2 types of herbivore. Rumination is thought to have evolved as a defence strategy (Kingdon, 1997), with ruminants minimising their exposure to danger by rapidly eating large quantities of food then retreating to the relative safety of tree cover to complete comminution (Janis, 1976). The defence strategy of equids is to flee from predators, so no survival advantage would have been derived from minimising eating time or by postponing comminution (Colbert, 1969).

6.4.3: Compensation for restricted feeding time

A major objective of this experiment was to attempt to identify the mechanisms by which animals compensate for restricted feeding time, and data from the current experiment showed how this was done. However, the effects of diet quality and ease-of-eating could not be distinguished unequivocally from each other.

Bite size per $M^{0.75}$ (Table 6.21) is largely dependent on the physical nature of the diet, the bite size when chopped alfalfa was fed being very much higher than when either straw or haylage was given to the animals. It appears from this experiment that all 3 species attempted to maximise bite size even when time did not constrain DMI. This was illustrated by the time-budgets for the animals when fed alfalfa (Table 6.9); animals spent the least amount of time eating but maintained the highest bite size per kg of metabolic live weight ($M^{0.75}$). In terms of energy expenditure, this strategy would be most efficient and is in agreement with the optimal foraging theory (Houston, 1993). These findings concur with the initial hypothesis that there is little or no opportunity to compensate for restricted feeding time by increasing bite size.

Bite rate was inversely related to bite size (Figure 6.4), as predicted by equation 6.1 (Ungar, 1996), although this relationship was non-linear. As DMI is directly proportional to both bite rate and bite size (Hodgson, 1986), maximising intake

involves a 'trade-off' between bite size and bite rate; results from the current experiment confirm this relationship. Chew rate showed little relationship (r^2=0.11) to bite size (Figure 6.5).

Results showed that the opportunity to compensate for restricted feeding time by increasing bite rate was limited, because an increase in bite rate was likely to be achieved at the expense of bite size. Moreover, it is more efficient for animals (in terms of energy expenditure) to attempt to maximise bite size rather than bite rate. Furthermore, the opportunity to increase bite rate is limited by the number of chews per bite, which is in turn, dependent on diet quality.

It appears that increasing ETPH is one of the few mechanisms available to herbivores to maintain DMI when access time to feed is limited. All animals in the current experiment showed considerable flexibility in terms of their circadian pattern of feeding activity (Figures 6.1 – 6.3). However, the opportunity to compensate for restricted eating time by increasing feeding intensity was limited by the nature of the feed. Animals fed diets with low intake characteristics (such as straw) have less opportunity to compensate for restricted time of access to food than when fed diets with high intake characteristics (such as alfalfa), because the former take more time to consume.

The effect of BCS on gut-dynamics was not successfully determined by this experiment. Further investigation is required in order to establish these affects.

Figure 6.4: The relationship between bite rate (bites per minute) and bite size (mg/bite/$M^{0.75}$) measured in cattle, donkeys and ponies fed alfalfa, haylage or straw .

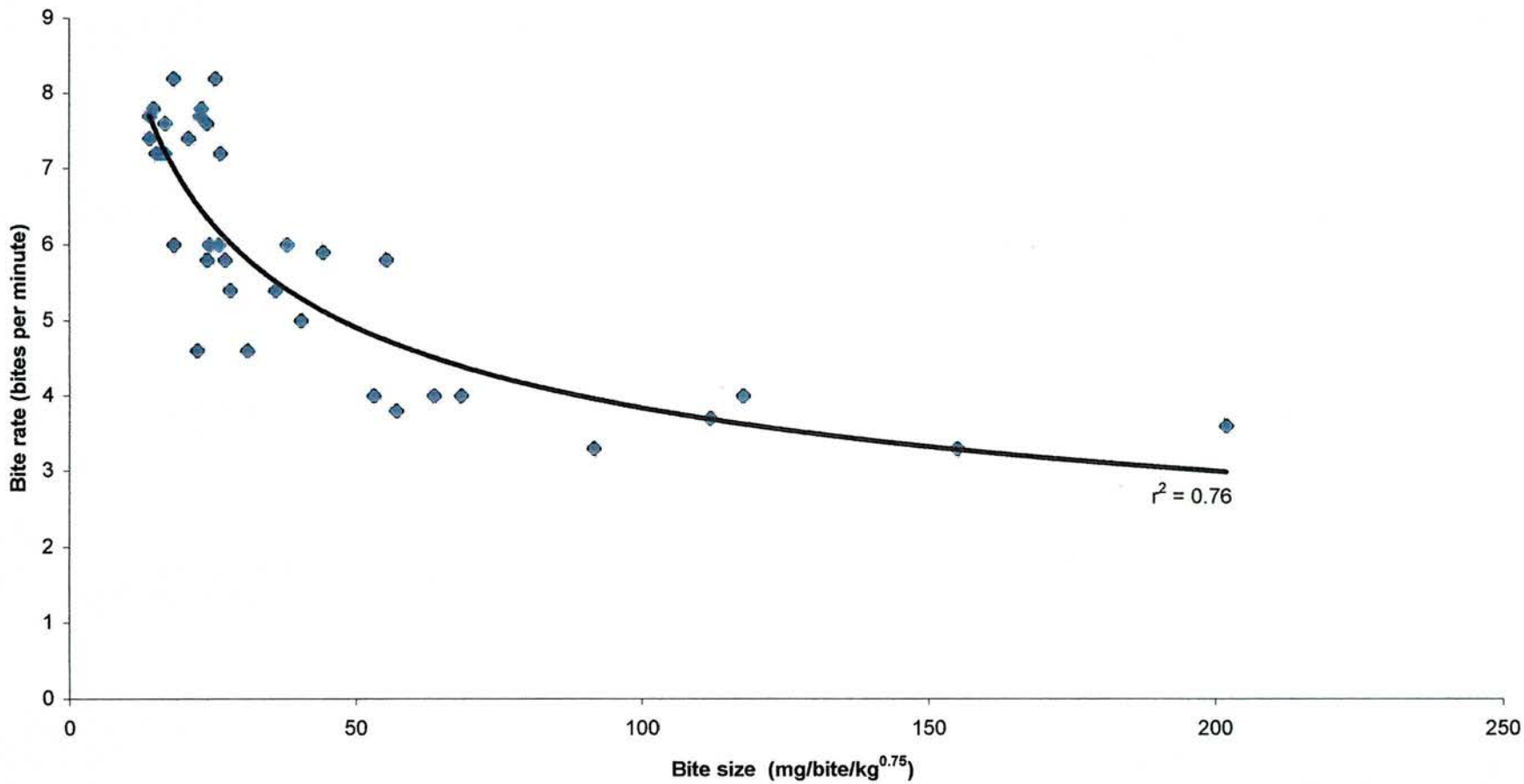
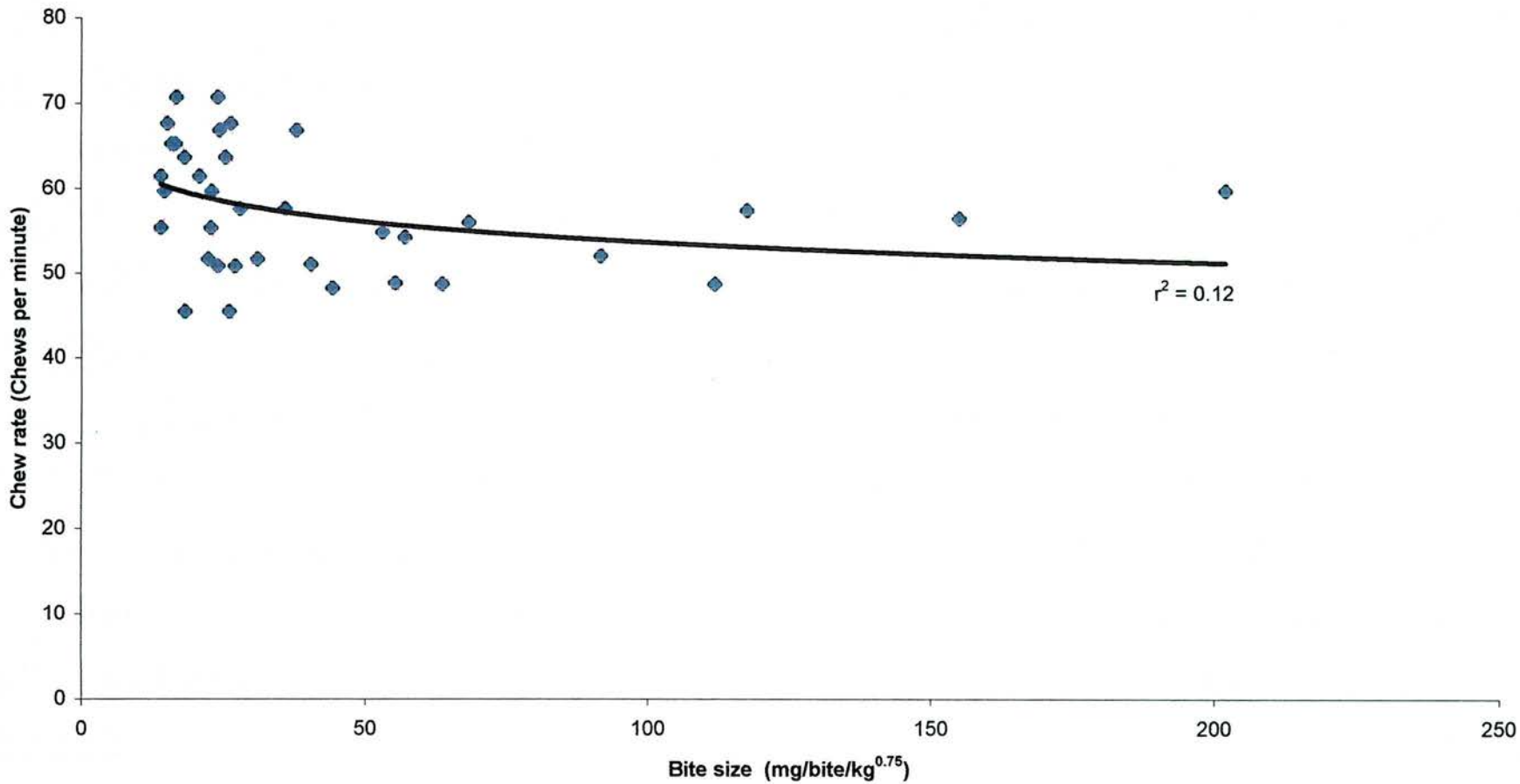


Figure 6.5: The relationship between chew rate (chews per minute) and bite size (mg/bite/$M^{0.75}$) measured in cattle, donkeys and ponies fed alfalfa, haylage or straw.



6.5: Conclusions

This experiment has illustrated several significant relationships between some behavioural components of food intake, in particular, the relationship between bite size and bite rate. Its seems unlikely that bite rate can be accelerated in order to compensate for restricted feeding time because this could only be achieved by decreasing bite size, which is energetically less efficient. Bite size and the number of chews per unit mass ingested appear to be closely related to the physical nature and fibre content of the feed fed to both cattle and the equid species.

The effect of restricted access to feed is likely to be more severe for equids than for cattle because rates of intake are smaller because of the need to complete comminution before swallowing.

Results from the current experiment suggest that the only opportunity to compensate for restricted feeding time in the 3 species of herbivore considered was by increasing the time spent eating within each hour. This opportunity was limited by the maximum intake rate of the diet fed, which was related to both the physical nature and diet quality.

CHAPTER 7:

TROPICAL RANGELAND STUDIES IN THE SOUTH-CENTRAL HIGHLANDS OF ETHIOPIA

7.1: Introduction

The results from the experiment reported in Chapter 6 showed that penned animals have little opportunity to compensate for RFT other than by increasing ETPH. Furthermore, the effect of RFT on DMI was dependent on the physical nature and quality of the food on offer.

An animal's ability to increase ETPH in response to restricted time of access to food or foraging is limited; time spent eating cannot exceed the time available for eating. Under rangeland conditions, the opportunity of compensating for RFT by increasing ETPH is further limited because animals must spend time foraging.

This chapter reports the results of comparing 2 methods of increasing the amount of eating time for cattle with the traditional communal grazing practices used in the southern-central highlands of Ethiopia. The first method increased the time available for eating by herding cattle to grazing at dawn and bringing them back at dusk, the second provided cattle with fodder in the kraal at night. The object of this comparison was to test whether these 2, low-cost methods of increasing forage availability resulted in increased DMI and improved live-weight gains. The study, also provided insights into the compensation strategies of cattle that had limited time available for eating under free-range conditions.

7.2: Materials and Methods

7.2.1: Location

Alemaya University of Agriculture is located in the southern-central highlands of Ethiopia, on the eastern escarpment of the rift valley (longitude 41° 5' east, latitude 9° 24' north) at 1980m above sea level. Rainfall distribution is bi-modal, with a short rainy season occurring between mid-February and April and a longer rainy season, from June to September (Thorton, 1972). Mean annual rainfall is ~ 736 mm (Shenkoru, 1987).

The study area was 450 ha on the eastern edge of Lake Alemaya. Most (80–85%) of the area was comprised of shallow slopes above the eastern shores of the lake, and was characterised by red soils (Regosol) with drought-tolerant grasses such as *Hyperrhenia, Andropogan, Sporobolus* and *Eluesine* species making up 80% of the plant species (Shenkoru, 1987). The remainder of the study area was a plain, close to the lake, and characterised by dark-brown alluvial soils (Fluvisols) with grass species such as *Pennisteum clandestinum* and sedges such *Cyperus escuientus* being dominant, especially in the area closest to the lake (Shenkoru, 1987).

7.2.2: Design

Three grazing access treatments (see details below) were applied to the group over the full period of the experiment from 20 March 1995 to 10 July 1995, a period of 16 weeks. This period was preceded by an adaptation period of 1 month. During the adaptation period, observers closely followed cattle so that the animals were completely used to human presence.

Over the 16-week period, two month-long detailed study periods were carried out, the first (EP1) between mid-March and mid-April, during the late dry season, and the second (EP2) between early June and early July, during the long rains. Sward condition during EP1 and EP2 is shown in Table 7.1. During the first 2 weeks of each of the detailed studies the DMI of the animals was estimated using external markers and measuring the *in vitro* DMD of the sward using the TT technique. In the second fortnight of each study period, behavioural observations were carried out to determine the time budget and diurnal behaviour patterns for time spent grazing. Two focal studies were carried out in the first and last week of each study period, in which the number of bites and steps were recorded.

A planned verification trial to measure recovery rates of internal and external markers was not completed due to unforeseen circumstances.

Table 7.1: Dry herbage mass, herbage dry matter, NDF, ADF, ADL, crude protein, gross energy and estimated ME of the sward during experimental period 1 (EP1) and 2 (EP2).

Treatment period	EP1	EP2
Dry herbage mass (g/m^2)	32.9	120.9
Dry matter content (g/kg)	641.9	559.4
Organic matter (g/kg DM)	916.5	905.1
NDF (g/kg DM)	616.7	653.3
ADF (g/kg DM)	315.8	335.9
ADL (g/kg DM)	48.9	50.0
Crude protein (g/kg DM)	120.5	157.2
GE (MJ/kg DM)	18.3	18.0
Estimated ME (MJ/kg DM) (MAFF 1987)	7.79	7.24

7.2.3: Animals

A group of 12 entire-male Ogaden cattle (starting live weight 291.8 kg) was selected from a herd of 50. Animals were selected to give 3 groups of 4 animals that were balanced in terms of live weight and maturity. In order to reduce the effect of herd size on feeding behaviour, a further 4 animals were selected from the main herd to act as companions to the 4 animals selected for the 12-hour grazing treatment (see below). The sub-herd of 16 animals was herded separately from the main herd during the day in order to facilitate handling and sampling. The sub-herd, with the exception of the treatment group receiving supplements, was reunited with the main herd when kraaled overnight.

All animals in the study group received the same tick-control treatment as the main herd. Tick control was enacted on an *ad-hoc* basis according to the availability of acaricide.

Animals were weighed once each week using a Ruddweigh K1200, portable weighbridge. Head collars were fitted to all the animals in the study group to facilitate handling and to partially accustom animals to the bite-meter equipment that would be used later in the experiment. Animals had access to water for 1 hour per day between 12:00 and 13:00 h.

The group of animals that received supplementary fodder (see below for details) was housed, when not at grazing, in 4 individual wooden stalls beneath a low roof made of corrugated steel sheets.

Each treatment group was assigned a colour, and each animal within the group had identification spots painted on each rump. This allowed observers to identify

individual animals at a distance in the field. Companion animals were marked with a green stripe down their back.

7.2.4: Grazing access

The group of 12 cattle was divided into 3 groups of 4 animals. Each group underwent a different grazing access treatment for the full course of the experiment. The 3 grazing access treatments were:

1. Traditional grazing treatment (Colour code: Orange)

   Animals had approximately 7-hour access to grazing per day, being released from the kraal at 08:00 h They were herded back to the kraal and allowed to drink at around 12:00 h for approximately 1 hour, and were returned to the kraal for the night at around 16:00 h. This pattern of grazing was similar to that of the main herd.

2. Extended grazing (Colour code: Green)

   Animals had approximately 11-hour access to grazing, being released from the kraal at 06:00 h, returning for approximately 1 hour around 12:00 h to drink, then returning to the kraal for the night around 18:00 h.

3 Supplementary fodder treatment (Colour code: Blue).

   Animals had approximately 7-hour access to grazing with the same grazing regime as the traditional grazing group. However, when this group returned to the kraal at night they were provided with bush-hay (Analysis: DM = 894 g/kg, OM = 933 g/kg DM, NDF = 753 g/kg DM, ADF = 454 g/kg DM, ADL = 57 g/kg DM, CP 43 g/kg DM, gross energy (GE) = 17.9 MJ/kg DM) to approximately 25% of their estimated daily DMI.

7.2.5: Ecological and climatic monitoring

Cattle, sheep and goats had continually grazed the study area during the previous growing season. The flood plain of the lake had been more heavily grazed than the surrounding hillside because cattle from neighbouring villages had also been grazed in this area.

The study area was nominally sub-divided into 2 ecological zones characterised by soil type and grass species. These zones corresponded to the alluvial plain at the edge of the lake (~60% of the grazing area) and the more drought-prone slopes (~40% of the grazing area). During the period between the 2 grazing studies the species composition of the grass and forb population of each zone was determined by botanical survey. Each zone was sampled in ~50 m wide blocks along a 'V' shaped transect at ~20 m intervals using a 1 m^2 quadrat fitted with a wire grid which formed 0.1 m^2 sub-divisions. The percentage cover of each species occurring within each quadrat was determined with the aid of the grid. Trees and bushes were excluded from the survey. The number of times each zone was grazed during the intake study was also recorded.

Climatic monitoring was carried out on a site that offered some security from vandalism some 1.5 km, from the study area. Rainfall, minimum and maximum temperatures and relative humidity were recorded at 08:00 h on every day of the study period. Field measurements of temperature and relative humidity were taken during the behavioural studies using a whirling hygrometer.

7.2.6: Measurements

Live weight

The animals were weighed once a week at approximately 12:00 h during the whole course of the experiment.

Dry matter intake, digestibility and faecal output

DMI was estimated using the external marker and *in vitro* method described in Chapter 2 (pages 15 and 27). Standard correction factors based on published faecal recovery values of CR_2O_3 (Mir, Kalnin and Garvey, 1989) were used in the estimation of FO by external markers.

Marker administration

To estimate FO, a single, 5g pellet of Cr_2O_3-mordanted-hay was administered to each animal once per day over a 12-day period at 12:00 h when the cattle returned to the kraal to drink. Mordanted pellets were made by the method described in Chapter 2 (pages 40–42). In place of the gelatine solution a little palm oil was added to each pellet, in order to bind the fibre. The pellets were then kept chilled until required for dosing. This process produced a firm pellet which could be readily loaded into a dosing gun, but which rapidly softened and collapsed under the heat and pressure from the animal's mouth. Even-chain alkanes were not used as an external marker because of the limited availability of C_{32} and C_{36} alkane from chemical suppliers at the time of the experiment.

Faecal sampling

Faecal samples were collected from animals by observers who followed them closely each day for the full 12-day dosing period. Where possible, 2 faecal samples were

collected each day from each animal, 1 during the morning and 1 during the afternoon. Samples were collected from the ground by an observer who was assigned 4 animals to follow from 08:00h until 12:00h and then from 14:00h until 16:00h. When an animal defaecated, the observer placed a sample of the faeces in a re-sealable plastic bag; further faecal samples were added to the bag as and when the animal defaecated.

At the end of each sampling day, each faecal sample was thoroughly mixed and a 100g sub-sample taken. This sample was dried at 100°C until constant weight and retained for analysis in the UK. This protocol provided 12 dried, faecal samples per animal at the end of the collection period. On return to the UK, the samples gathered on the final 5-days of the collection period were analysed in duplicate for their chromium content according to the method of Uden, Colucci and van Soest (1980). Five replicate faecal output values were calculated using equation 2.4 (Chapter 2) for each animal; one for each of the daily samples analysed. A correction factor of 0.90 was applied to the faecal outputs to account for incomplete recovery of the external marker (Mir, Kalnin and Garvey, 1989).

In addition, for each animal, a weekly-pooled sample made up of additional 50-g sub-samples of fresh material taken from each daily sample was dried at 60°C. This provided 2 pooled weekly samples per animal per intake study, which were retained for chemical analysis in the UK.

Sward sampling

A representative sample of material that the animals consumed was obtained by taking at least 6 samples per day from the sward, for the final 8 days of the intake

study. The structure of the sward was such that the selection opportunities for the cattle were limited to bite depth and patch choice. The sward samples were, therefore, taken from a $1m^2$ quadrat placed immediately in front of one of the grazing cattle. The herbage enclosed by the quadrat was clipped to a height of 2 cm above ground level and placed in a large re-sealable plastic bag of known weight. On return to the lab the fresh herbage mass was determined by weighing the sealed plastic bag and subtracting the initial empty bag-weight. The herbage was then cut into 2–3 cm lengths with clippers, mixed and a 100g sub-sample taken. The sample was dried at 60°C to constant weight in a forced-draught oven and retained for chemical and *in vitro* DMD analysis in the UK. A smaller herbage sample of known weight was dried in a forced-draught oven at 100°C to constant weight, in order to calculate DM after drying. This sample was then discarded.

7.2.7: Behavioural observations

A detailed behavioural study was carried out during the final 2 weeks of each experimental period. Because of the problem of security in Ethiopia, it was not possible to carry out any behavioural observations at night, although an attempt was made to monitor the night-time feeding behaviour of the stall-fed cattle with the telemetric bite meters described in Chapter 3.

Scan observations

Scan-sampling observations were carried out at 5-minute intervals during three-hour long observation sessions staggered between 06:00 h and 18:00 h, with each observation session being replicated 3 times. This provided a composite 12-hour behaviour profile for each animal, made from a total of 12 three-hour observation

sessions. A Psion organiser data recorder (datalogger) was used to collect the data. During the period of the day, when all animals were grazing together (between 08:00 h and 16:00 h), scan-observations were recorded for all 12 animals simultaneously. On the occasions when groups were not herded together, treatment groups were observed separately from one another.

Three behavioural criteria were recorded. These were position (lying, standing, walking), oral activity (eating, drinking, ruminating) and attitude (tense, alert, resting, sleeping). Time spent in each of these activities per hour was calculated from the total number of times an activity occurred, multiplied by the average observation interval during the hour.

Focal observations: Step and bite counts

Focal observations were carried out in the first and last week of each study period. During each of these observation periods data were collected over a 5-day period. The observations consisted of recording the number of steps and bites that occurred within a 5-minute period. The data were collected and recorded by trained observers equipped with 2, hand-held, tally counters, a countdown-timer and a notebook.

Focal observations were carried out at 08:00, 11:00, 14:00 and 16:00 h. On the morning of each observation day, observers were assigned a treatment group to observe. The treatment group assigned to each observer was rotated on a daily basis in an effort to partially balance any observer effects and to eliminate bias. Each observer recorded the behaviour of each treatment group at least once during the focal-observation week.

During each 5-minute observation period, the observer would count each bite and step with the aid of the 2 tally counters. Bites were defined as the actual prehension of food. The sound of prehension, as well as visual criteria, was used to help distinguish when a bite had occurred. Chews and exploratory mouth movements were not counted. A step was defined as a positive movement of the right foreleg, resulting in a forward motion of the animal's body; fidgeting and pest-related movements of the right foreleg were not included.

Step and bites were only recorded when animals were actively feeding. An animal was considered to be feeding actively when it appeared that eating or food-seeking activity were of primary priority. If active feeding did not occur within an hour of the start of a particular observation period, the step and bite measurements were recorded as zero.

Mean bite rate (bites per minute), step rate (steps per minute) and bites per step for each of the observation weeks were calculated for individual animals for each of the daily observation sessions. Mean bite rate, step rate and bites per step were also calculated for the morning and afternoon grazing sessions.

A forage sample was taken, using a $1m^2$ quadrat, from the grazing site during each step and bite observation session, using the same method as that used to collect feed samples during the intake study. The fresh and dry herbage mass of this sample was calculated and a representative sub-sample retained for proximate analysis in the UK.

HORAS bitemeter measurements

The telemetric bite meter described in Chapter 3 was used to record data from the cattle during the hours of darkness. Time spent ruminating and, in the case of the

supplementary feeding treatment, time spent eating were determined from these observations.

7.3: Results

Ecological and climatic monitoring

The maximum and minimum temperatures, relative humidity and rainfall during the 20 weeks of the study are shown in Figures 7.1, 7.2 and 7.3. Most of the rain that occurred during the experimental period fell in April, after the intake study in EP1 had been completed. This rainfall to some degree disrupted the collection of the behavioural data but had little effect on the availability or quality of the forage (Table 7.2). Botanical composition, herbage mass and sward quality of the sloped and alluvial zones is shown in Table 7.3.

The prolonged dry spell during June and July, following a period of rapid sward growth and subsequent senescence after flowering, resulted in a rapid fall in sward quality from the intake study phase to the behavioural study phase.

Table 7.2: Dry herbage mass, dry matter content, organic matter, NDF and crude protein content of sward during the intake study and behaviour study phases of EP1 and EP2

Treatment period	EP1		EP2	
Nature of study	Intake	Behaviour	Intake	Behaviour
Weeks	1 –2	3 - 4	1 –2	3 - 4
Fresh herbage mass (g/m^2)	92	135	274	420
Dry herbage mass (g/m^2)	33	42	121	141
Dry matter content (g/kg)	642	689	560	664
Organic matter (g/kg)	916.5	905.6	905.1	917.0
NDF (g/kg)	616.7	688.4	653.3	693.0
Crude protein (g/kg)	120.5	141.0	157.2	86.9

Figure 7.1: Minimum and maximum temperatures showing seven day rolling average at Alemaya, Ethiopia, March -July 1995; experimental periods 1 (EP1) and 2 (EP2) are numbered

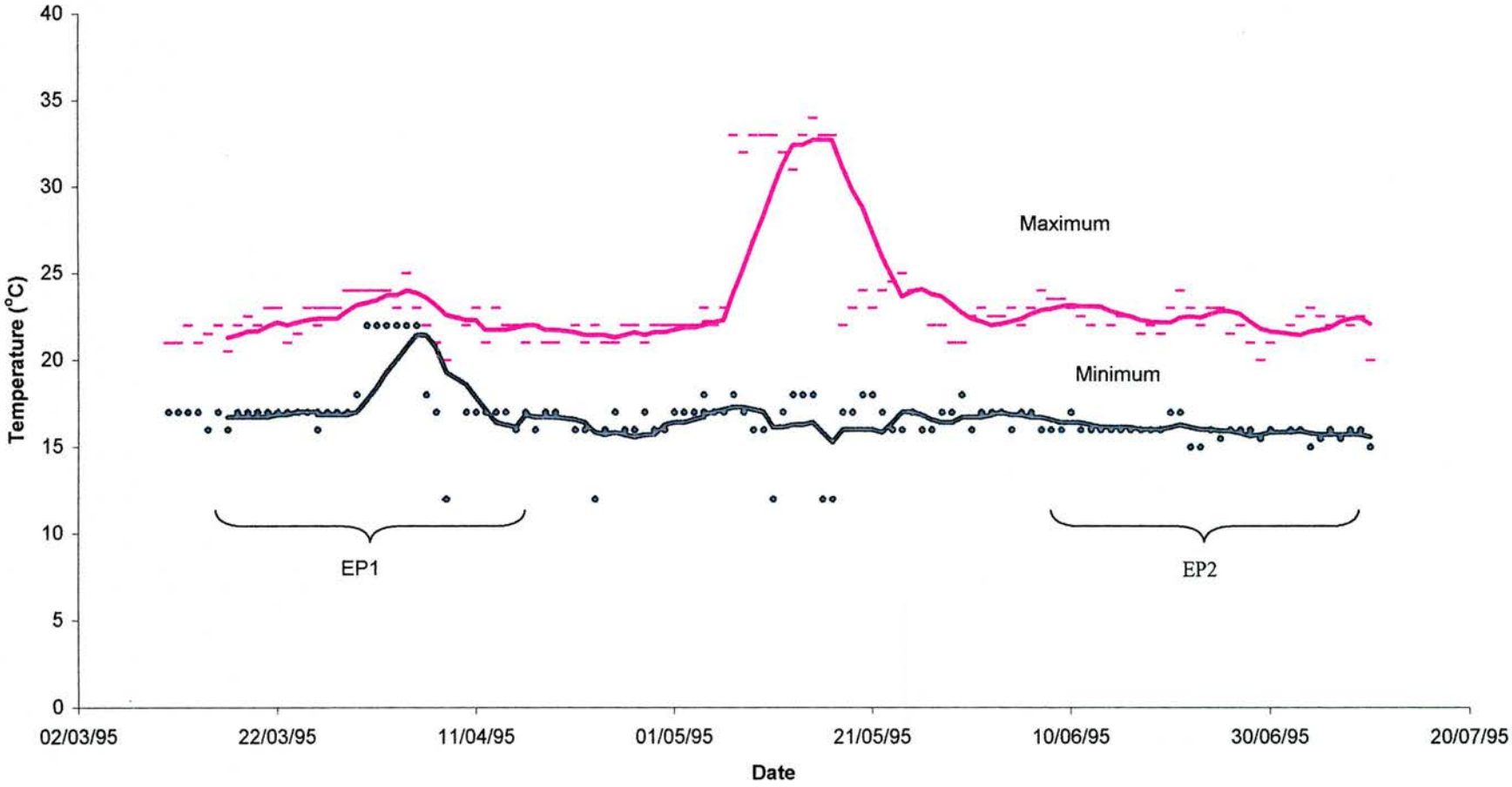


Figure 7.2: Relative humidity (RH%) at 08:00 h showing seven day rolling average at Alemaya, Ethiopia, March -July 1995; experimental periods 1 (EP1) and 2 (EP2) are numbered

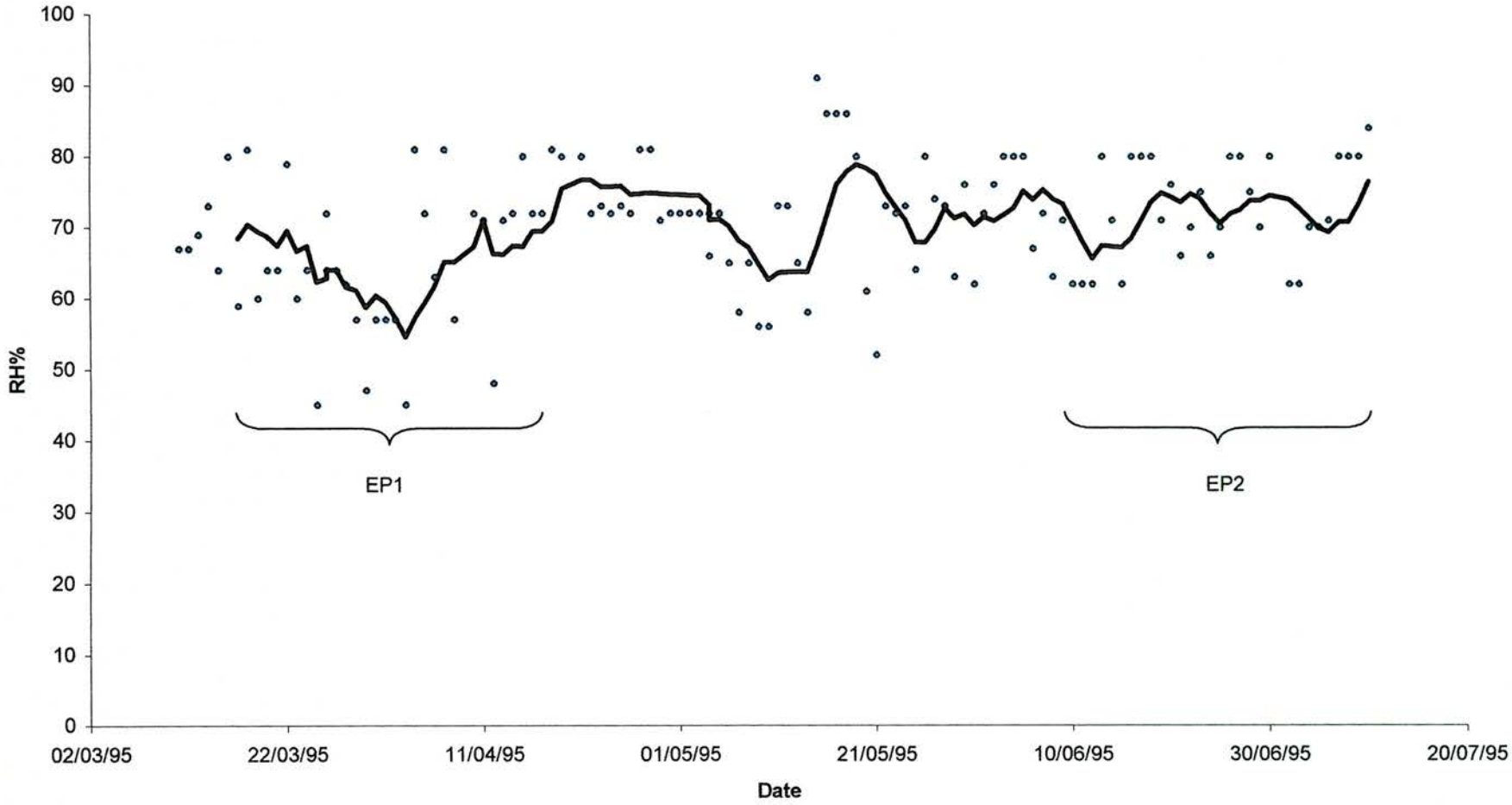


Figure 7.3: Weekly rainfall (mm) at Alemaya, Ethiopia, March -July 1995; experimental periods 1 (EP1) and 2 (EP2) are numbered

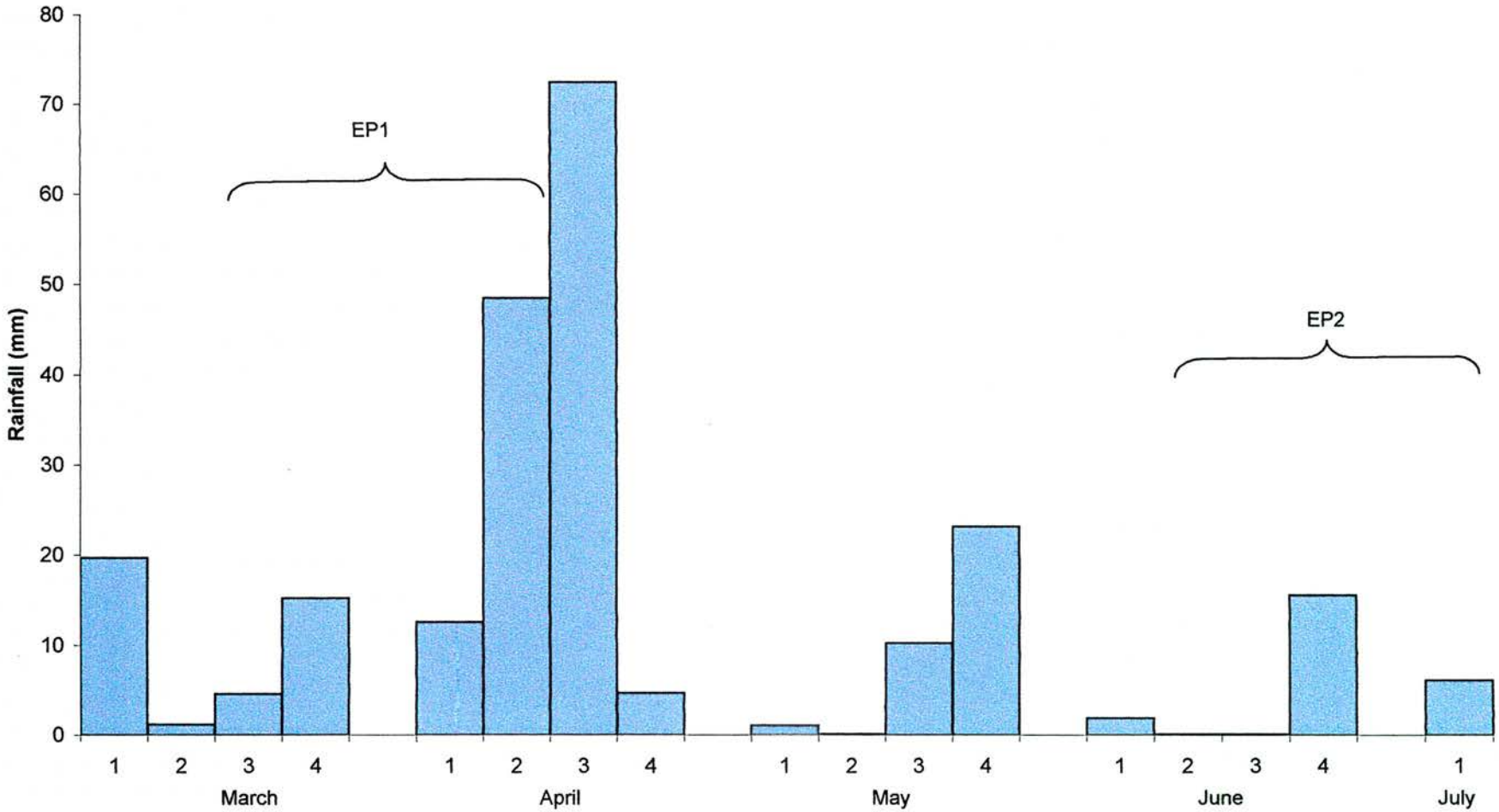


Table 7.3: Mean percentage cover of the ten most common herbage species in the two ecological zones used for grazing, showing mean herbage mass and sward quality during EP1 and EP2 at these sites.

Grazing area	Slope zone	Alluvial zone
Species	*Mean cover (%)*	
Chlories prieurii	15	0
Cyndon dactylon	4	10.
Cyperus esculentus	0	13
Eleusine floccifloia	9	16
Hypparrhenia dissoluta	10	0
Hypparrhenia filipenendia	15	0
Pennisetum glabrum (adoensis)	11	12
Pennisetum clandestinum	0	42
Pennisetum villosum	14	0
Trifolium rupplianum	4	7
Other grasses species	2	0
Bare Ground	16	0
Number of quadrats sampled	59	187
	Sward quality	
EP1		
Dry matter (g/kg)	351	342
Dry herbage mass (g / m^2)	35	42
Organic matter (g/kg)	902	912
NDF (g/kg)	674	581
Crude protein (g/kg)	82	140
EP2		
Dry matter (g/kg)	623	379
Dry herbage mass (g / m^2)	59	129
Organic matter (g/kg)	897	899
NDF (g/kg)	645	590
Crude protein (g/kg)	69	114

Live weight

Live weight changes during the course of the 16-week experiment are shown in Figure 7.4; there was no significant difference between treatments. The changes in live weight as a percentage of starting live weight, are shown in Figure 7.5.

Dry matter digestibility, faecal output and dry matter intake

The *in vitro* DMD of the diets were 0.70 and 0.67 for EP1 and EP2 respectively, Within-sample variation of the *in vitro* DMD was less than 2%. The within-sample variation of DMD estimated using ADL as an internal marker was too great to provide a reliable estimate of DMD, the deviation of digestibility coefficients from the mean being of the order of 10-15%. Mean values of DMD estimated with ADL were 0.79 and 0.74 for EP1 and EP2 respectively.

There were no significant differences in total DMI or DMI at pasture between any of the treatments (Table 7.4). Overall, animals ate significantly more ($P<0.05$) during EP1 (102.1 g per $kg^{0.75}$ per day) than during EP2 (94.0 g per $kg^{0.75}$ per day), although this difference was not measured in DMI at grazing, and resulted mainly from the supplemented group eating more hay during EP1.

Figure 7.4: Live weight (kg) of three groups of cattle with different access time to feed

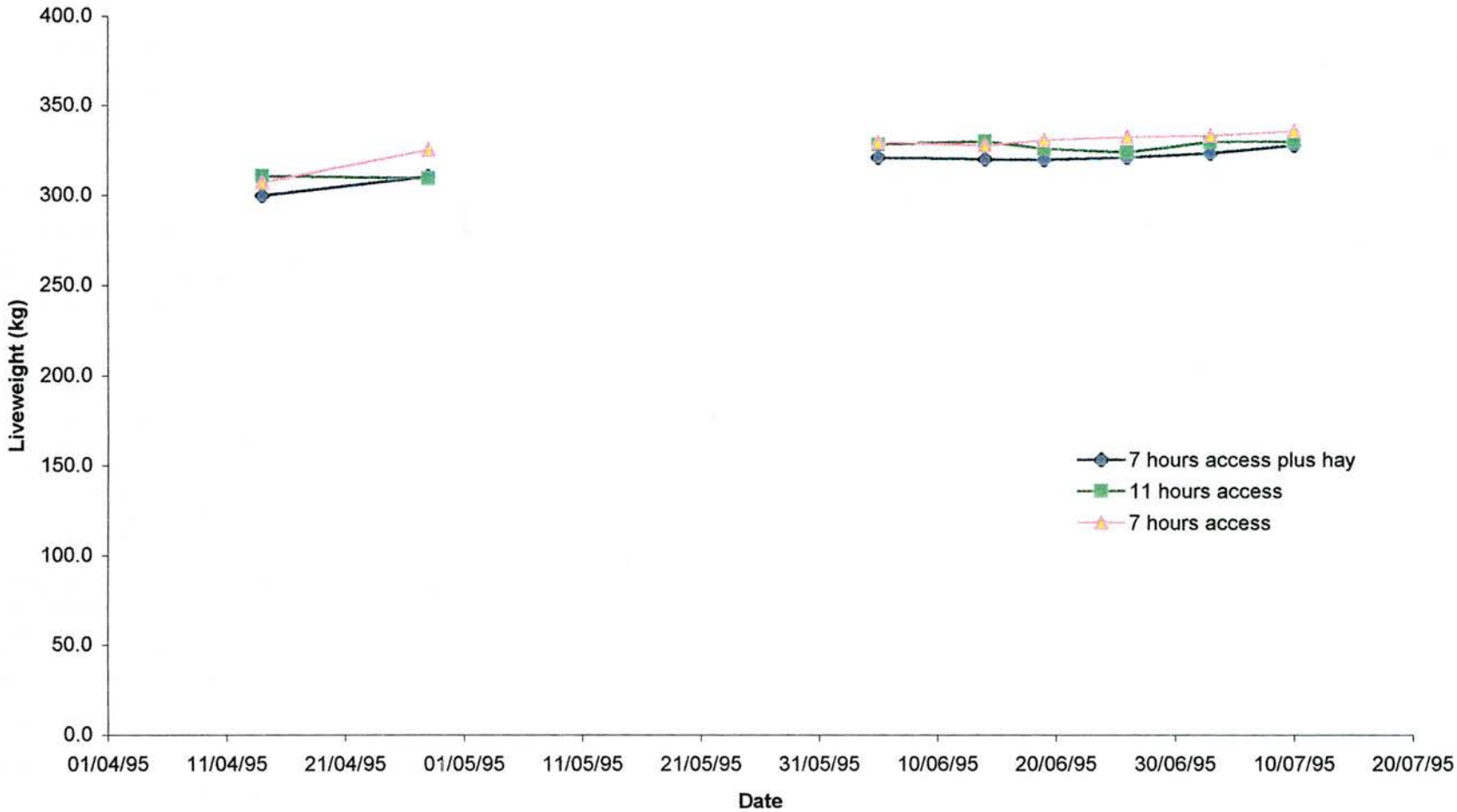


Figure 7.5: Change in live weight as a percentage of initial live weight (± s.e.) of three groups of cattle with different access time to feed

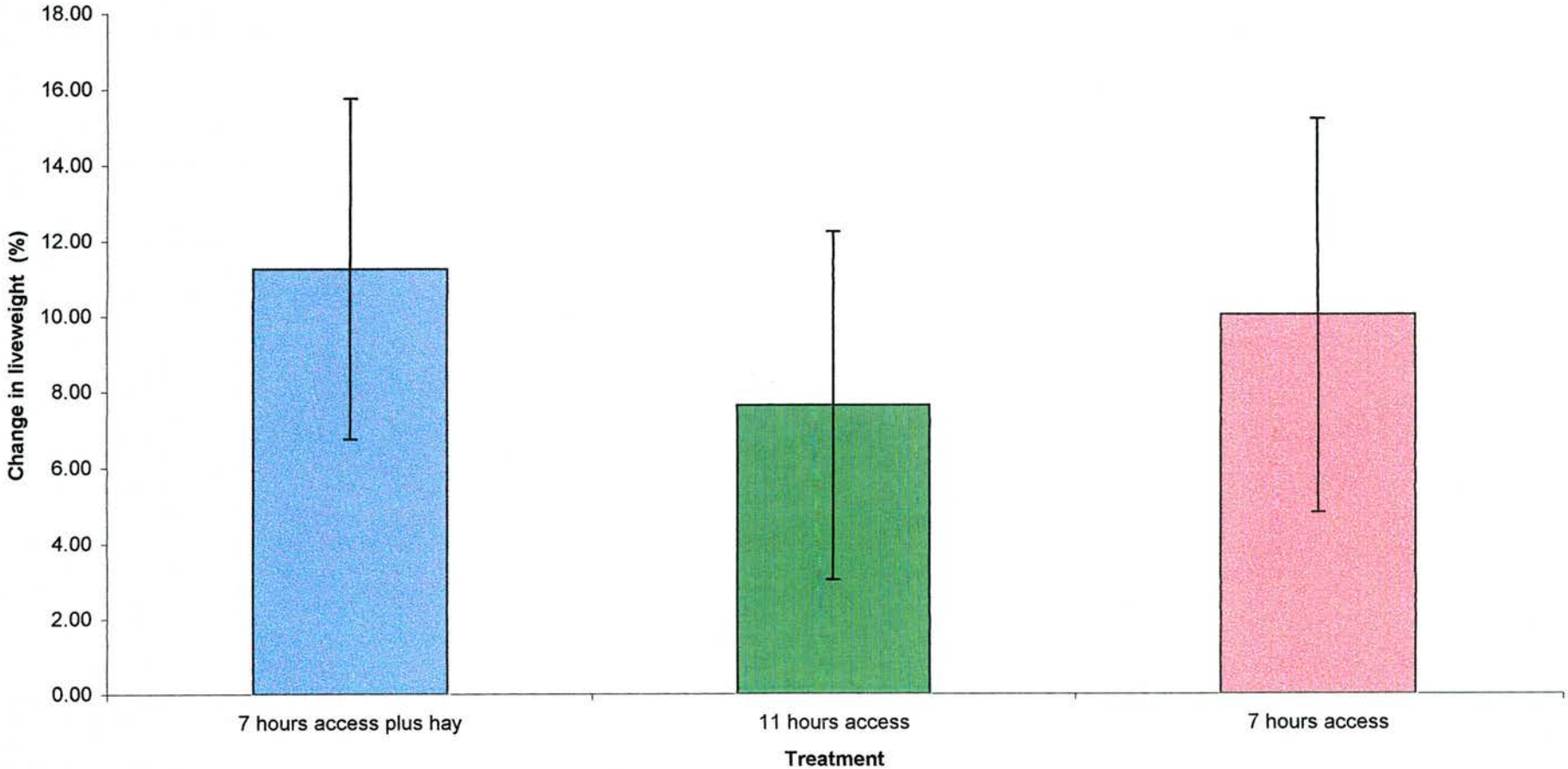


Table 7.4: Daily dry matter intake (g per kg $M^{0.75}$) of hay and forage by cattle in the three treatment groups, during EP1 and EP2 (±s.e.).

Grazing access	7 hours plus hay supplement	7 hours	11 hours
EP1			
Hay	13.8 (1.2)	- -	- -
Forage	98.4 (1.8)	101.0 (8.3)	106.8 (6.0)
EP2			
Hay	4.5 (0.4)	- -	- -
Forage	97.8 (3.5)	97.8 (4.0)	86.6 (4.0)

Time budgets

Recording of 'attitude attributes' during the behavioural observation proved problematic as the descriptors 'tense', 'alert', 'resting' and 'sleeping' were not sufficiently well-defined for observers to make objective assessments. For completeness results are presented in Table 7.5.

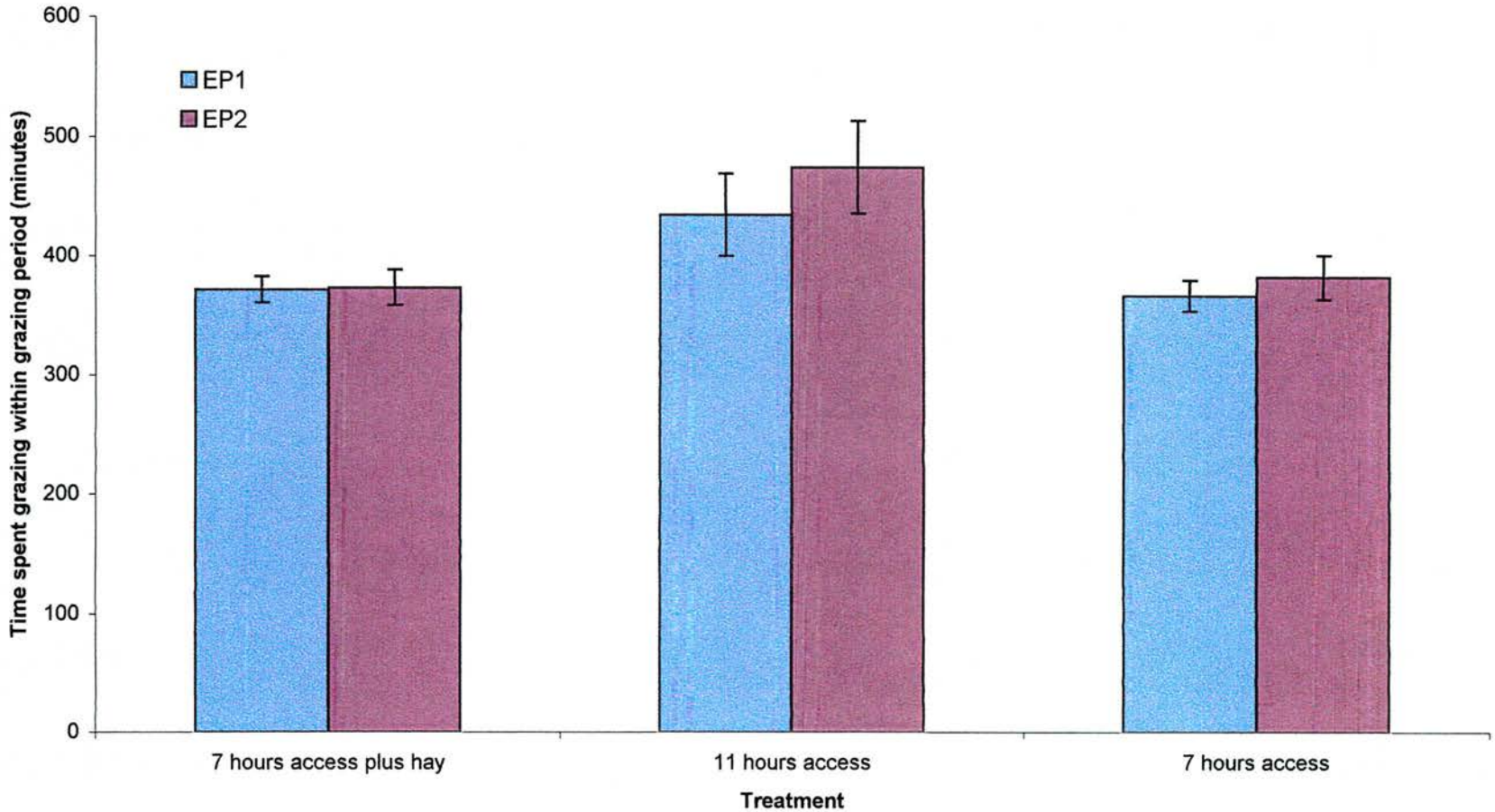
There was no significant treatment effect on time spent lying down, standing or walking. However, there was a significant ($P<0.001$) period effect on time spent walking and standing (Table 7.5).

There were significant effects of treatments on time spent grazing. The treatment group given 11-hour access to grazing spent significantly ($P<0.05$) more time grazing than the other 2 treatment groups. There were no significant differences between EP1 and EP2 in the time spent grazing. There were no effects of treatment or period on the time spent ruminating during the 12-hour observation period (Table 7.5).

Table 7.5: Time (minutes) spent lying, standing, walking, eating, ruminating, alert, resting or sleeping by three treatment groups between 6:00 and 18:00 h during EP1 and EP2 (±s.e.).

Grazing access	7 hours plus hay supplement	11 hours	7 hours
EP1			
Position			
Lying	72 (17.8)	161 (20.1)	72 (8.5)
Standing	545 (24.3)	453 (9.9)	552 (11.2)
Walking	104 (10.0)	106 (17.1)	97 (4.5)
Oral activity			
Eating	410 (11.0)	434 (34.6)	367 (12.9)
Ruminating	97 (15.6)	73 (4.7)	87 (11.9)
Drinking	11 (0.8)	12 (5.8)	7.1 (2.0
None	200 (8.2)	182 (6.3)	256 (5.9)
Attitude			
Alert	525 (5.0)	505 (3.8)	500 (26.5)
Resting	190 (3.6)	122 (7.0)	209 (26.4)
Sleeping	5 (1.6)	88 (9.4)	6 (1.9)
Other	0 (-)	5 (2.1)	5 (1.1)
EP2			
Position			
Lying	92 (33.6)	63 (15.4)	79 (23.2)
Standing	571 (36.9)	579 (20.5)	563 (13.6)
Walking	57 (4.6)	78 (5.8)	78 (11.7)
Oral activity			
Eating	395 (15.5)	453 (39.3)	378 (19.5)
Ruminating	82 (7.2)	40 (11.7)	71 (15.1)
Drinking	0 (-)	12 (6.3)	7 (2.0)
None	194 (18.4)	180 (27.9)	224 (10.6)
Attitude			
Alert	681 (15.1)	728 (22.3)	685 (3.4)
Resting	23 (14.6)	34 (19.6)	7 (3.8)
Sleeping	9 (12.4)	0 -	2 (1.3)
Other	12 (13.2)	20 (9.6)	25 (5.5)

Figure 7.6: Time (minutes) spent grazing within grazing period (± s.e.) of three groups of cattle with different access time to feed during the late dry season (EP1) and early, long wet season (EP2)



Circadian pattern of eating and rumination

The circadian patterns of grazing and rumination can be seen in figures 7.7 – 7.10. During EP1 the treatments had little effect on ETPH, except where total grazing time was physically limited by the treatment regimes. Comparison of the ETPH of the 3 treatment groups during the hours of common grazing (08:00 h – 12:00h and 13:00 h – 17:00 h) showed no significant difference (Figure 7.8). The ETPH of the 11-hour-per-day grazing group during the non-common grazing hours (06:00–08:00 h and 17:00–18:00 h) was significantly different ($P<0.01$) from the ETPH of this group during the common grazing hours (24.1 and 45.0 minutes per hour respectively). In EP2 the pattern of ETPH in the 11-hour per day grazing group was quite distinct from that of the other 2 groups, with greater between-hour variation (Figure 7.8). ETPH of the 2 treatment groups with 7-hour access to grazing was consistently higher (mean ETPH 47.5 minutes per hour) than that of the group with 11-hour access to grazing (41 minutes per hour), although this difference was not significant. The mean ETPH during the non-common grazing hours and the common grazing hours of the 11-hour per day grazing group were virtually identical (41.7 and 41.4 minutes per hour respectively).

Figure 7.7 Time (minutes) spent grazing per hour (± s.e.) by three groups of cattle with different access time to feed during the late dry season (EP1)

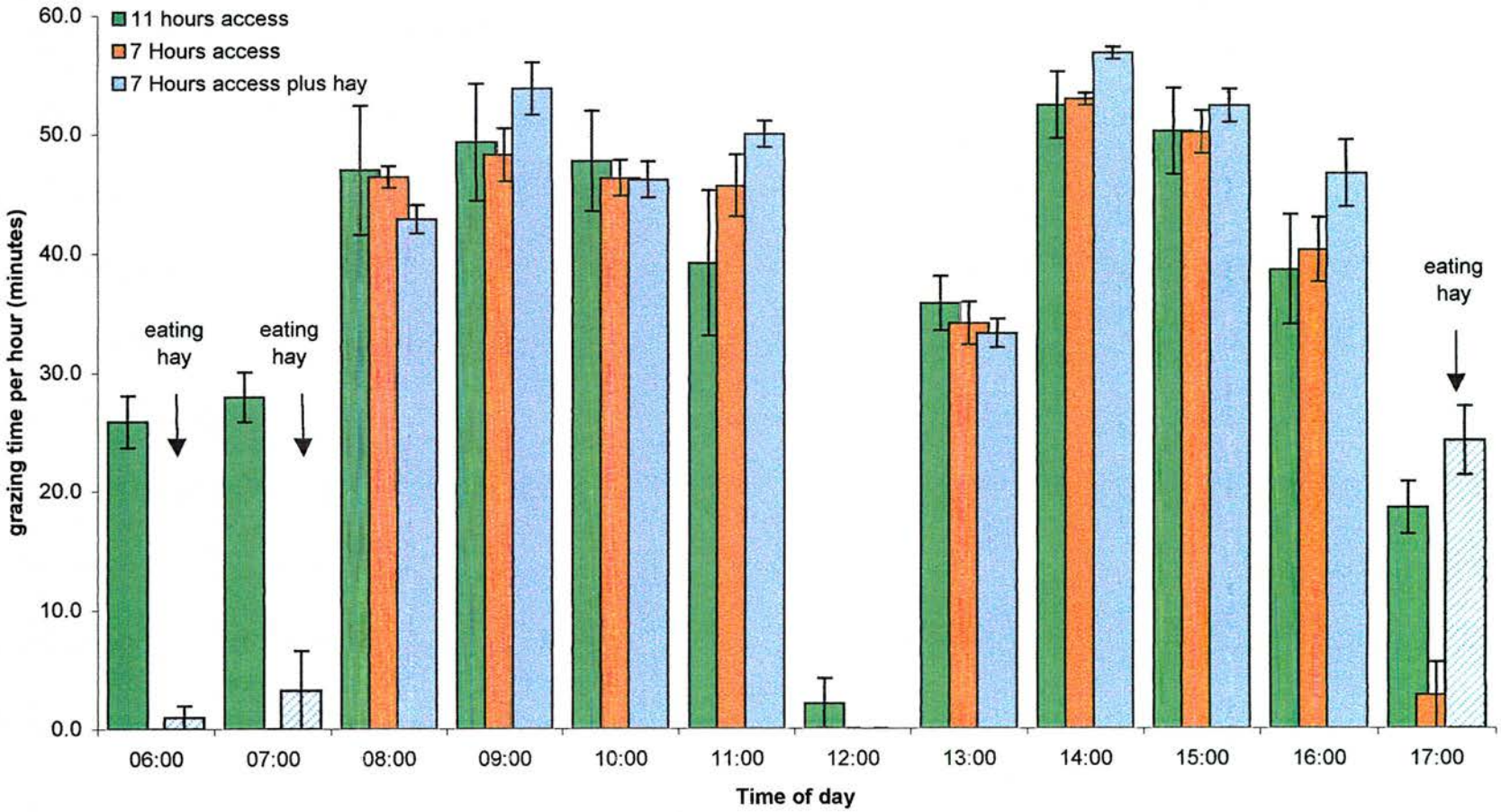


Figure 7.8 Time (minutes) spent grazing per hour (± s.e.) by three groups of cattle with different access time to feed during the early long wet season (EP2)

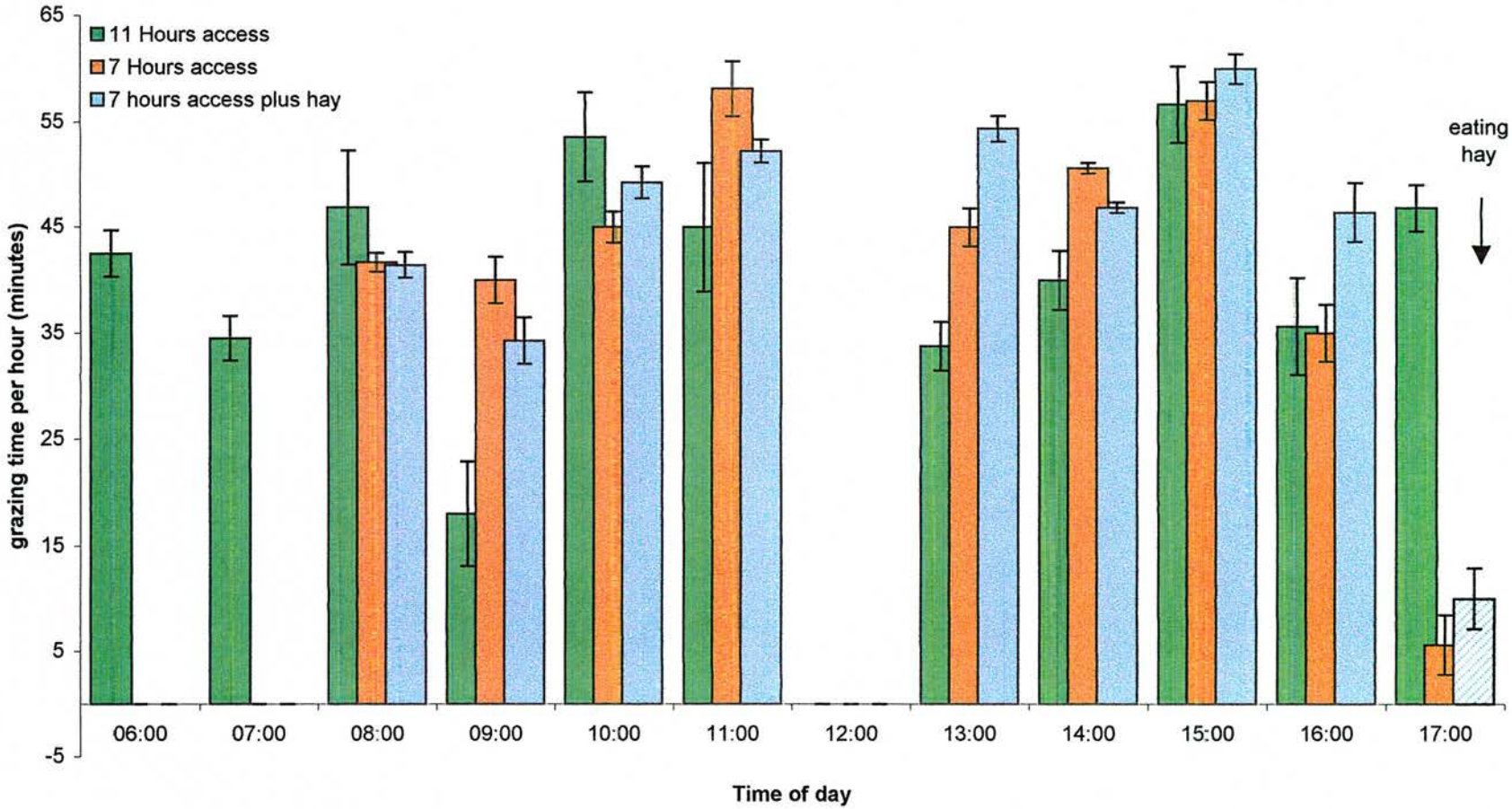


Figure 7.9 Time (minutes) spent ruminating per hour (± s.e.) by three groups of cattle with different access time to feed during the late dry season (EP1)

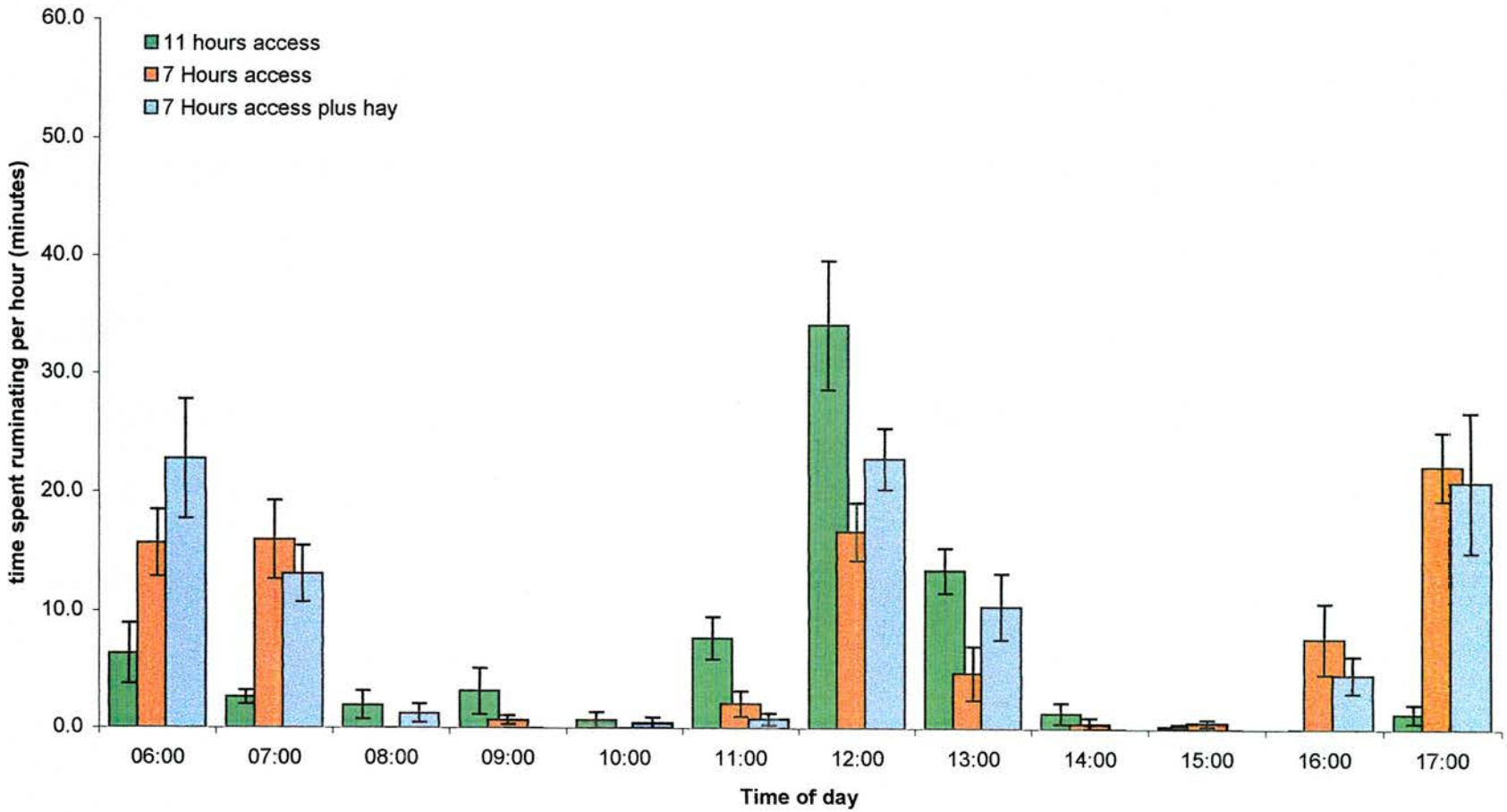
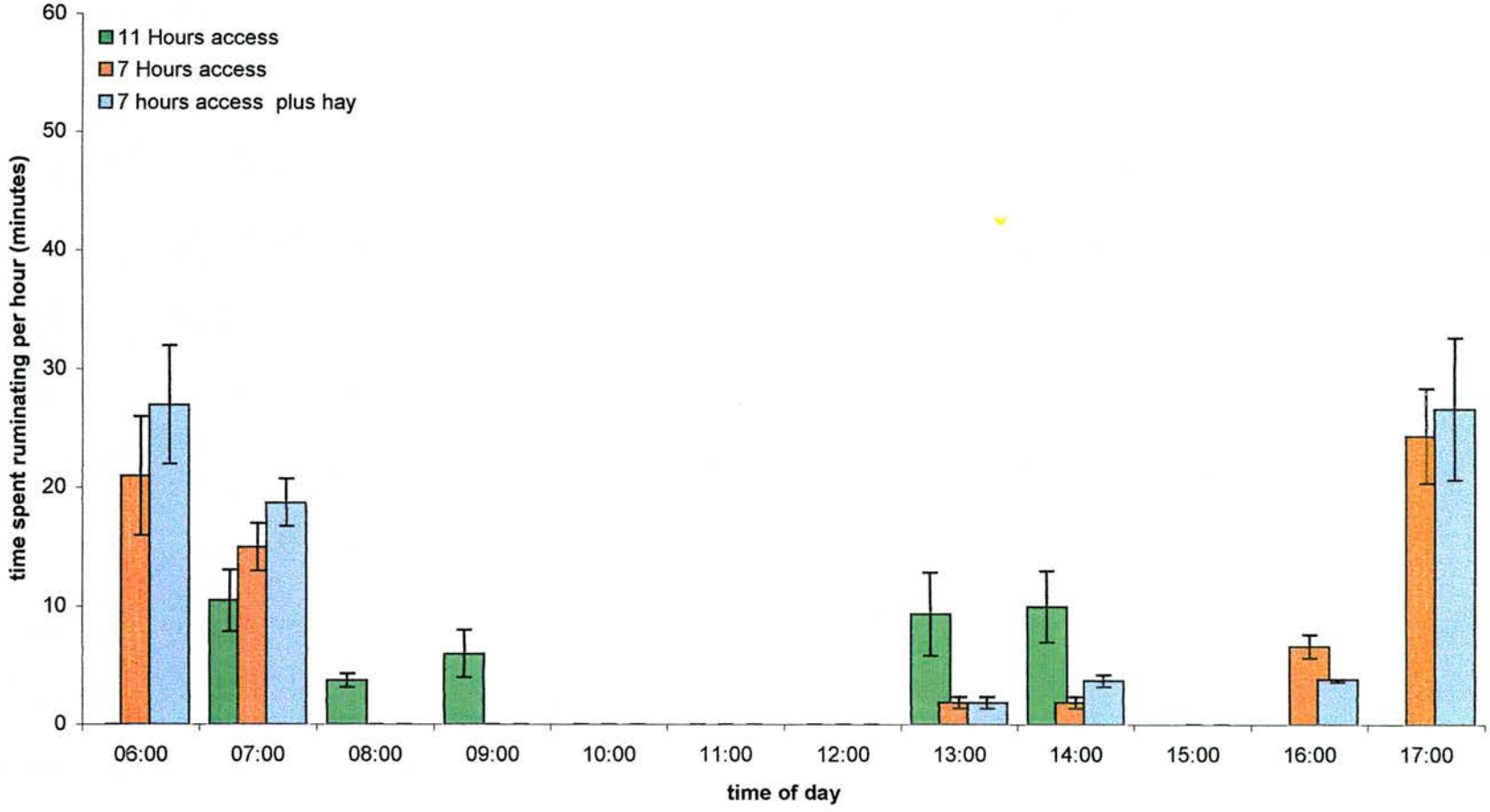


Figure 7.10 Time (minutes) spent ruminating per hour (± s.e.) by three groups of cattle with different access time to feed during the early long wet season (EP2)



Focal observations

There was no significant effect of observer or observation week on the bite and step rates recorded during either EP1 or EP2 (Table 7.6).

Non-parametric, statistical analysis (Mann-Whitney 'u' test, Minitab version 7.1) of bite rate, step rate, number of bites per day and number of steps per day showed no significant differences between EP1 and EP2. Non-parametric statistical analysis of treatments was not possible due to the limited number of animals in each treatment. Parametric statistical analysis (ANOVA) of bite size showed no significant differences between treatments, but very highly significant $P<0.001$) differences between EP1 (6.50 mg/bite/kg $M^{0.75}$) and EP2 (5.4 mg/bite/kg $M^{0.75}$).

7.4: Discussion

Treatment effects on live weight changes

Access time to grazing had no effect on live weight change during the course of the whole experiment from mid-March to mid-July, indicating that there was no advantage in extending the amount of time available for eating under conditions local to the south-eastern highlands of Ethiopia. The experiment was carried out over a period when sward quality was moderate to good, and herbage mass was increasing (Table 7.2). Had this experiment been carried out over a period when feed resources were limited, the treatments may have affected live weight.

Table 7.6: Bite rate (bites per minute), step rate (steps per minute), bites per step, bites per day, steps per day and bite size (g) of the three treatment groups during EP1 and EP2 (± s.e.).

Grazing access	7 hours plus hay supplement	11 hours	7 hours
EP1			
Bites per minute	41 (0.6)	34 (1.2)	44 (1.3)
Steps per minute	10 (0.4)	7 (0.6)	9 (1.8)
Bites per step	0.87 (0)	1.03 (0.1)	1.07 (0.2)
Bites per day	16878 (252)	14592 (861)	16081 (866)
Steps per day	4065 (228)	3193 (535)	3437 (813)
Bite size	0.4 (0.05)	0.5 (0.07)	0.4 (0.04)
EP2			
Bites per minute	46 (0.8)	39 (0.4)	45 (1.1)
Steps per minute	9 (0.3)	8 (0.1)	8 (0.2)
Bites per step	1.06 (0)	1.01 (0)	1.15 (0)
Bites per day	17078 (435)	18551 (453)	17003 (481)
Steps per day	3256 (161)	3711 (301)	2968 (153)
Bite size	0.4 (0.05)	0.4 (0.05)	0.4 (0.03)

Reliability of dry matter intake estimation

Estimates of DMI using *in vitro* techniques to estimate DMD and Cr_2O_3 as an external marker to estimate FO were considerably higher than those predicted by the ARC (1980) intake model (66–77 g DM per kg $M^{0.75}$) for diets with a metabolizibility (q) of between 0.4 and 0.5. However, if live weight changes were used to estimate energy intake, the DMI of cattle fed diets with q-values of between 0.4 and 0.5 was

calculated to be between 68 and 95 g DM per kg $M^{0.75}$ (Lawrence and Pearson, 1999); values closer to those estimated by the *in vitro* / FO technique used in the current experiment.

Treatment effects on dry matter intake and feeding behaviour

Providing additional time for grazing had no effect on total DMI. Dry matter intake of animals given 11-hour access to grazing was not significantly different from those that had only 7-hour access. Animals with 11-hour access to grazing spent more time foraging than those animals with only 7-hour access. However, there was no significant change in ETPH during the hours of common grazing. The only consistent difference between the feeding behaviour of the 11-hour access group and that of the other 2 treatment groups was in bite rate; it was lower in the group given more time to graze (Table 7.6). Bite size and total number of bites per day showed no consistent differences between treatments.

The data from this experiment indicate that cattle will utilise additional grazing time if it is provided, but this does not lead to increased DMI or live-weight gain. Cattle appear to slow down their rate of intake when they have more time to graze by decreasing bite rate but they still strive to maintain maximum bite size. Whether this decrease in bite rate was due to an increase in the number of chews per bite, an increase in the bite-to-bite interval (due to more careful selection of forage) or simply due to a more 'leisurely attitude' to grazing cannot be established from the data obtained in this experiment. Whatever the reason for the decline in bite rate, there was no production advantage to increasing the time available for grazing by cattle during the seasons and in the location in which the experiment was carried out.

The greater bite rate of cattle during both 7-hour treatments implies that these animals were expending more effort to achieve the same levels of DMI as the cattle on the 11-hour treatment. The extent to which bite rate can be accelerated in response to limited grazing time has not been established in this experiment. However, as maximum bite rate is dependent on both the quality and physical structure of the sward the extent to which increased bite rate can compensate for restricted grazing time is limited (Ungar, 1996).

Giving cattle access to low-quality hay during the hours of kraaling also did not have any effect on DMI or live-weight gain. The feeding behaviour of cattle that received hay supplement was identical to those that only had 7-hour access to grazing. During EP1, supplementing tended to depress intake at grazing but not during EP2. Under the sward conditions operative during this experiment, feeding poor quality hay in the kraal cannot be recommended as a method of improving animal performance. Furthermore, in communal grazing conditions, kraal feeding of hay is disadvantageous to individual farmers because it results in cattle depending on the pastoral resource less and making use of fodder which farmers have made a considerable effort to harvest and store.

Effects of season on dry matter intake and feeding behaviour

There were no effects of season on forage DMI by cattle during this experiment. The intake study in EP1 occurred at the very end of the dry season, when it was predicted that both sward quality and herbage mass would be at a minimum; these assumptions were not supported by the analysis of sward (Table 7.1, 7.2 and 7.3). Herbage mass was low during EP1 but sward quality was moderately high (Table 7.1, 7.2 and 7.3). The intake study in EP2 was at the start of the long rainy season and followed a 6-

week period when little rain had fallen. Sward quality was predicted to be moderate at this stage and herbage mass was expected to be high; these assumptions were supported by sward analysis (Table 7.1 and 7.3). The quality of the sward during EP1 and EP2 was very similar, but there were major differences in herbage mass available to the animals (Table 7.3).

The unexpectedly high quality of the sward during EP1 was probably due the dominance of *Pennisetum clandestinum* in the alluvial zone, the zone most frequently grazed by cattle (Table 7.3). *P. clandestinum* is a deep-rooted perennial grass that forms a dense turf (Humphreys, 1980) and maintains a moderate feeding value even when mature (Göhl, 1992).

Dry matter intake during EP1 was not limited by bite size despite low herbage mass. Bite size was not measured during this experiment, but was derived from DMI, bite rate and grazing time measurements (Table 7.6). The estimations of bite size in this experiment were close to those measured by Stobbs (1973) in cattle grazing on tropical sward, and exceeded 0.3 g OM per bite below which, bite size limits DMI.

The ability of the cattle to maintain DMI during EP1, despite the low herbage mass of the sward, was due to the structure of the sward in the alluvial zone where *P. clandestinum* was dominant (Table 7.3). *P. clandestinum* has a low habit (Humphreys, 1980), that produces a sward with high bulk density. Bulk density is a measure of the three-dimensional distribution of the herbage mass within the sward canopy and shows a strong positive correlation with bite size (Ungar, 1996). The cattle in this experiment were, therefore, able to achieve high bite weights because most of the herbage mass was concentrated in a narrow horizon, seldom more than 15 cm high.

The seasonal variation in sward conditions had no effect on the DMI of cattle during this experiment. This was because 1) sward quality remained good during the dry season and 2) the botanical composition in the alluvial zone provided a sward of high bulk density during the dry season which allowed the cattle to achieve bite sizes which did not limit DMI. Both of these conditions resulted from the proximity of the grazing area to the lake.

7.5: Conclusions

Estimation of DMI by using *in vitro* DMD and an external marker was considered to be a valid approach. Cattle with 7-hour access to grazing achieved the same DMI as cattle with 11-hour access or with 7-hour access plus hay supplement. There was no apparent advantage to extending feed or to providing hay supplement.

Cattle given 11-hour access utilised the additional time to graze, spending longer eating, but decreasing their rate of intake by taking fewer bites per minute. This implies that cattle with limited access to grazing respond by increasing bite rate. However, because physical nature and quality of the sward limit maximum bite rate, this ability to compensate for restricted grazing time is limited. Severely restricting grazing times together with poor sward conditions could result in a depression of DMI amongst traditionally managed cattle in Africa.

In this experiment, providing cattle with hay in the kraal did not improve live-weight gain or DMI under the prevailing sward conditions. Where sward conditions or grazing management do not limit DMI there is no advantage to the individual farmer in giving hay to cattle in the kraal. Indeed, this is counter-productive because the additional labour input results in cattle eating less of a common pastoral resource that the farmer can utilise with little effort and no cost. Where DMI is limited by sward

conditions or management there may be an advantage in providing hay in the kraal, but this has still to be shown.

Seasonal effects of sward condition were not fully examined in this experiment because of the proximity of Lake Alemaya to the grazing site. However, the 2 different levels of herbage mass that occurred in this experiment did not effect DMI. There was insufficient difference between sward quality during the 2 experimental periods to distinguish any effect of sward quality.

Traditional grazing management systems in the southern-central highlands of Ethiopia provide adequate time for grazing cattle to achieve a DMI that allows a modest daily live-weight gain. Under the conditions found at Alemaya, increasing the amount of time or providing supplementary feed did not result in improved productivity. However, the performance of this grazing system under more arduous rangeland conditions has not been established and more long-term studies are required to investigate this under a broader range of environmental conditions.

CHAPTER 8:

RANGELAND STUDIES OF CATTLE AND DONKEYS AT MATOPOS RESEARCH STATION, ZIMBABWE

8.1: Introduction

The rangeland study carried out in Alemaya, Ethiopia with cattle during 1995, showed that restricted grazing time did not affect DMI if sward quality was moderate and herbage mass remained high. The proximity of the grazing study area to Lake Alemaya reduced the effect of seasonal rainfall on sward condition because the water content of the soil remained high. These conditions are not typical of rangeland ecosystems, which usually depend entirely on rain as a source of water. The environmental conditions during the second study, in Southern Zimbabwe, were more typical of tropical rangeland where there were strong seasonal effects on sward condition. This study was carried out using cattle and donkeys during the late dry season of October 1996 and the mid wet season of February 1997.

One aim of this study was to continue the work started in Ethiopia and to gather more information on the effect that sward condition and season have on cattle performance and DMI. This study also presented an opportunity to investigate the 'natural' foraging behaviour of cattle when given 24-hour access to grazing.

Donkeys were also included in this study because they are becoming an increasingly popular choice as draught animals amongst the farmers of Southern Zimbabwe (Nengomasha, 1997). Little is known about the feed requirements of these animals or of the effect of traditional grazing practices on their subsequent performance. A principal aim of the Zimbabwean study was to investigate the feeding behaviour of

free-range domesticated donkeys in order to understand how these animals used the rangeland feed resource.

Also in this study a comparison between cattle and donkeys foraging the same area of rangeland was carried out with the aim of determining the implications of different management systems on the performance of the 2 types of herbivore.

8.2: Materials and Methods

8.2.1: Location description

Matopos Research Station covers some 28,000 ha and is located 30 km south of Bulawayo (longitude 20.5° south, latitude 28.5° east) at 1350-1400 metres above sea level. The mean annual rainfall is stated as 580 mm although, with the prevalence of droughts in recent years, a more realistic estimate of expected rainfall would be closer to 450 mm per year (Smith and Ncube, 1995). The wet season is between mid-November and March, and little rain precipitates outside this period. The hottest period is between September and March (average daily temperature range 14-28°C), and the coldest between June and July (average daily temperature range 2 -21°C) with frequent frosts during this period.

The southern end of the station, where the study was carried out, was characterised by small granite kopjes (small rocky hills) with shallow rocky soils (feriallitic sands and sandy loams), and sodic and black (vertisol) clays in the more fertile areas. The natural vegetation consisted of open-woodland and grassland. The experimental area enclosed a diverse range of vegetation types, including areas that had previously been cultivated, dry river beds, well established acacia and mopane woodland and several small kopjes. *Aristida* and *Eragrostis* species were the dominant grasses in

the more sandy areas, with *Terminalia* species being the most common tree. In the sodic soil areas, *Sporobolus* species of grass dominated with *Acacia karro* being the most common tree. In the black clay areas *Hyperrhenia* species of grass prevailed with *Acacia karroo* being the most common tree.

An area of enclosed rangeland measuring approximately 230 ha was set aside for the experiment. Donkeys and cattle foraged together within the enclosed area, and were not herded other than for short periods at the time of kraaling or when experimental procedures had to be carried out (see below for details). All other domestic herbivores were excluded from the area during the course of the experiment. Wild ungulates such as greater kudu *(Tragelaphus strepsiceros)* and water buck *(Kobus ellipsiprymnus)* were occasionally observed in the experimental area and resident populations of cape rock hyrax *(Procvia capensis)* were common in the rocky regions. Other small herbivore species, such as spring hare *(Pedetes capensis)* were likely to be present but in fact were never observed.

8.2.2: Study schedule and experimental design

The schedule comprised a grazing study divided into 2 experimental periods. During the interval between experimental periods the faecal recovery rate of Cr_2O_3 and C_{36} external markers was determined by total faecal collection using the same animals that were used in the grazing studies.

The first grazing study period (ZP1) was carried out in October 1996, at the end of the dry season, when both sward quality and herbage mass were at their lowest. The second grazing study (ZP2) was carried out between mid-February and mid-March 1997, during the mid-wet season, when sward quality should have been moderate

and herbage mass was greatest. However, there was a lull in the rains during late December 1996 and early January 1997, which resulted in premature senescence of many of the grass species before the second experimental period began and giving a lower sward quality than expected .

Each grazing study period lasted 3 weeks. In the first week of the study period, scan and focal behavioural observations were made. On the first day the dosing schedule began and was continued for a further 12 days. In the second week faecal samples and diet samples were collected. Further scan behavioural observations were made, including night observations if there was a full moon. In the third week, scan behavioural observations were completed and post-collection focal behavioural observations were made. Sward quality and abundance was measured in the first and third week as described below.

8.2.3: Ecological and climatic monitoring

The site was surveyed by a rangeland ecologist at the start of the study. The main grass and trees species were identified and listed. The experimental area had been grazed for the previous year by only 8 bulls. At the start of the experiment, at the end of the dry season, there was an abundance of dry forage (154.7 g/m^2 mean dry herbage mass) (other than in the area immediately adjacent to the kraals, handling pens and trough). On the basis of dry herbage mass, the theoretical carrying capacity (CC) of the area was calculated to be 1.5 ha per tropical livestock unit (250 kg) (ILCA, 1986). This very high value was due to under-utilisation in the previous growing season rather than a true reflection of the sustainable productivity. Although the concept of CC has little meaning in semi-arid, communally-based

grazing systems (Bayer and Waters-Bayer, 1998), it is used here as a convenient expression of the relevant abundance of forage.

Ambient climatic data for the study area were recorded daily during each experimental period. Temperature (maximum and minimum) and relative humidity (maximum and minimum) were monitored by placing an electronic thermometer/hygrometer at animal head height (approximate 1.5 m) in a tree close to the kraal and handling pens. Local rainfall was measured using a rain gauge placed in a clear area, several metres from the tree containing the thermometer/hygrometer. A small fence was erected around the rain gauge to protect it from the attention of animals.

8.2.4: Animals

Twelve mature male castrate donkeys (initial live weight 153.2 kg,) and twelve 2-year old Tuli, male castrate cattle (initial live weight 233.3 kg) were selected from the available pool of animals (20 donkeys and 30 cattle) to provided balanced species groups in terms of live weight and age. Donkeys that were known to have a tendency to escape from enclosed areas were excluded from the selection process.

All the animals were dosed with Panacur anthelmintic (Coopers Ltd) and a pour-on acaricide (Coopers Ltd) in the first week of the adaptation phase of each experimental period. The acaricide treatment was repeated every 21 days, to prevent tick reinfestation. The normal tick control method for cattle was for them to be dipped every 7 days. However, since it was not possible to dip the donkeys it was decided to adopt a tick control method that could be applied equally to both species and would not cause excessive disruption to the experimental routines.

Animals were weighed at the end of each working week using a Ruddweigh K1200 (Ruddweigh, Australia), portable weighbridge, at the experimental site. Head collars were fitted to all animals to facilitate handling and also to partially accustom the animals to the bite-meter apparatus that would be used in the experiment.

The animals were introduced to the enclosed grazing area 1-month before the start of each study period. The rangeland access treatments were applied from the start of each adaptation phase. Workers were assigned to follow the animals closely during this phase to allow the animals to become accustomed to the close proximity of humans.

Animals had free access to water 24 hours per day and water was provided in the kraals for those that had restricted access to grazing. Animals tended to visit the water trough as a group around midday and also when herded back to the kraal in the evenings.

A row of 4 kraals, each measuring 5 x 5 metres was built to accommodate the animals which had restricted access to grazing. Four animals of the same species and from the same treatment group were placed in each kraal.

Each treatment was assigned a colour, and each animal in the treatment group had a large identification number in the colour of its treatment painted on both sides of its rump. This allowed the observers in the field to identify animals at a distance.

8.2.5: Rangeland access

During ZP1 and ZP2 there were 3 rangeland access treatments, 4 cattle and 4 donkeys being allocated to each of these treatments as follows:

a.) 23-hour access (Control)

Animals nominally had continuous 24 hour access to the rangeland. However, they were herded to the handling pens at 08:00 h and 16:00 h each day during the intake studies in order to administer the marker pellets and to collect faecal samples, reducing free access to rangeland by approximately 45-60 minutes per day.

b.) 11-hour access

Animals nominally had 12-hour access to the rangeland being released from the kraal at 06:00 h and penned for the night at 18:00 h. Administration of the marker and faecal collection was carried out at the same time as for the control group, thereby reducing access to the rangeland by approximately 45-60 minutes.

c.) 8-hours access (Traditional)

Animals had 8-hour access to the rangeland, being released from the kraal at 08:00 h and brought to the handling pens at 16:00 h. Administration of the marker and sampling took place during the period of confinement and thus had no effect on access time to rangeland.

8.2.6: Sward monitoring

In order to measure changes in herbage mass and sward quality within and between ZP1 and ZP2, 25 steel rod quadrats measuring 1 metre by 2 metres, divided laterally to form two 1-m^2 sub-quadrats were constructed and placed at random throughout the study area. Trees and bushes were excluded from the quadrats. The position of each

quadrat was marked with a 1.5-metre metal rod with a numbered plastic flag attached to it, so it could easily be located and identified.

In the first and third week of each study period, one of the 2 sub-quadrats of each quadrat was harvested to 2 cm above ground level. The harvested material from each sub-quadrat was placed into paper bags of known weight. In order to reduce weight loss by evaporation the paper bags were placed in re-sealable plastic bags of known weight and the bags sealed. At the laboratory the bags from each sub-quadrat were weighed and the fresh yield of herbage calculated. The paper bags were then removed from the plastic bags and placed in a forced-draught oven at 60°C until constant weight was achieved. The paper bags plus samples were then re-weighed in order to determine dry matter content and dry herbage yield for each sub-quadrat. The dry samples were ground using a mill fitted with a 1-mm screen, thoroughly mixed and a 100g sample taken. These samples were subsequently analysed at the University of Edinburgh to determine organic matter, acid detergent fibre (ADF), neutral detergent fibre (NDF), acid detergent lignin (ADL) and crude protein (CP) content according to the methods of the Association of Official Analytical Chemists (1990) and Van Soest and Robertson (1985).

8.2.7: Diet sampling and analysis

A representative sample of the diet selected by the animals from the rangeland was obtained by a rigorous sampling procedure during the final 5 days of the dosing schedule. This procedure provided samples that represented both the range of plants the animals selected and the relative quantities of each in the diet.

Three observers were assigned to follow animals closely between 08:00 h and 12:00 h and between 14:00 h - 16:00 h. The animals were followed closely for a month before collection began to habituate them to the procedure. Each observer was assigned 4 animals from one treatment group in a day. The treatment group assigned to each observer was rotated each day of the 5-day collection period to reduce any effect of observer bias. Operators were trained to observe the animals closely and to make a mental note of not only the species selected, but also the horizon from where the bite was made.

Observers were instructed to follow one animal in their assigned group for 15 minutes in each collection hour. During each 15-minute observation period an individual animal was followed closely, and a sample (approximately 50g) of what it selected to eat was taken approximately every 3 minutes. The individual samples were placed in a labelled paper bag, which was then closed by stapling. Five samples per hour per animal were collected for a total of 6 hours per day (30 samples). At the end of the 5-day collection period there were 150 individual paper bags containing sward samples for each animal.

At the end of each sampling day the paper bags containing the individual samples were placed in a force-draught oven and dried to constant weight at 60°C. At the end of the sampling week the samples were sorted according to animal, sampling day and time of sampling. Each individual sample was then ground through a mill fitted with a 1-mm screen and placed in a small, plastic, re-sealable bag.

To construct a pooled sample for the full week that accurately reflected the diet of each animal on a quantitative basis, 1-g sub-samples from each individual sample

were pooled to produce a single composite sample for each animal. These samples were used to determine the OM, GE, NDF, ADF, CP, ADL and alkane content of the diet of each animal. A 5-g sub-sample from the composite diet sample from individual animals was taken and pooled with those of other animals of the same species given the same rangeland access. These samples were used for *in vitro* digestibility studies.

Tilley and Terry's (1963) method was used to determine the *in vitro* DMD of a single pooled sample from each species/rangeland access group. Rumen liquor was used as a source of inoculum with all samples so that *in vitro* DMD values would reflect only the differences in diet selectivity between donkeys and cattle, rather than the ability of each species to digest the selected diet.

A quality index (QI) for each diet sample was calculated based on the crude protein, NDF and IV-DMD using Equation 8.1:

$$QI = \frac{CP}{NDF} * IVDMD * 1000 \qquad \text{(Equation 8.1)}$$

QI allowed the quality of each diet to be expressed as a single number simplifying the statistical analysis of the diet quality data.

8.2.8: External marker dosing and faecal sampling

A 5 g pellet of ALCMF was given to each animal twice per day at 08:00 h and 16:00 h for 12 days. Dosing began 7 days before faecal samples were collected in order to allow the output of marker to reach equilibrium.

Faecal samples were collected twice daily at 08:00h and 16:00h for the final 5 days of the dosing period. They were collected directly from the rectum of the animals and placed in re-sealable plastic bags. Samples were dried to constant weight at

60°C in a forced-draught oven and ground through a 1-mm screen. Sub-samples (5 g) were taken from each sample and mixed to form a single composite weekly sample per animal that was used for analytical purposes. The alkane and chromium content of faecal samples were determined at the Edinburgh laboratory .

8.2.9: Faecal recovery of external markers

The 12 cattle and 12 donkeys used in the grazing studies were housed in individual pens for a period of 24 days in the period between ZP1 and ZP2. During this time, they were fed *ad libitum* on a diet of poor quality hay containing 904g DM kg^{-1} (Table 8.1) and given free access to water.

Table 8.1: Composition of the hay fed (g/kg DM) to cattle and donkeys during the Zimbabwe verification trial.

Nutrient	g/kg DM
Organic Matter	946
Neutral-detergent fibre	785
Acid-detergent fibre	497
Crude protein	30
Ash	54

After a period of 12 days adaptation to the *ad libitum* hay, the animals were dosed twice a day at 08:00h and 16:00 h for 12 days with a 5 g ALCMF bolus. A total faecal collection was made for the final 5 days of the dosing period. Fresh faeces were weighed, thoroughly mixed and a 200-g sample taken. The dry matter content of the sample was determined and the total daily faecal dry matter output was calculated.

Faecal grab samples were taken at 08:00 h and 16:00 h directly from the rectum. The dry matter content of the faecal grab samples was determined by the change in weight before and after drying to constant weight in a forced-draught oven at 60°C. Individual faecal grab samples were pooled and retained for chromium and alkane analysis.

External marker recovery was determined by calculating the mean daily input of the external markers from their concentration in the ALCMF and the mean weight of ALCMF dosed per day (10 g). Mean daily output of both markers was estimated from faecal concentration and mean daily dry FO. Recovery rates were calculated according to the method of Momont *et al.* (1994). Estimated FO using both external markers was calculated using Equation 2.4 (Chapter 2).

8.2.10: Dry matter intake

Dry matter intake was estimated in free-ranging animals using three methods simultaneously, as there was no single method available which was considered entirely reliable (see Chapter 2). Use of multiple methods provided an indication of reliability of the DMI estimations and highlighted any likely source of error. The methods used were:

i) The alkane-pair method using C_{36} alkane as the dosed marker, C_{35} as the natural marker and Equation 2.6 to calculate intake (Chapter 2).

ii) The double-marker method using C_{36} alkane or Cr_2O_3 as an external marker and ADL as an internal marker. Dry matter intake was estimated using Equations 2.3, 2.4, and 2.5 (Chapter 2). A correction factor derived from the

recovery rate of both external markers was applied to faecal marker concentrations in order to adjust for incomplete recovery.

iii) The faecal output markers together with an *in vitro* DMD method using Equations 2.3 and 2.5 to calculate intake (Chapter 2). The same correction factors as used in method ii) were applied to the faecal concentrations of external markers. *In vitro* DMD was determined using the Tilley and Terry (1963) method for the cattle diets, and the adapted Tilley and Terry method, PP+N, described in Chapter 2 for the donkey diets. A single *in vitro* DMD value was determined for each species/rangeland access group based on the pooled sample for each of these groups described in Section 8.2.7.

8.2.11: Behavioural Observations

A detailed behavioural study was carried out during both ZP1 and ZP2. The objectives were to determine time budgets, circadian variation and changes in herbage selection during each period.

Scan sampling

Scan sampling observations were made at 5-minute intervals during daylight hours. During darkness, when the animals had settled, observation intervals were reduced to every 15 minutes. Daylight scan sampling sessions were between two and four hours long, and were designed to 'fit around' the normal daily routine. Night-time observation sessions were over 12 hours long. A Psion datalogger was used in the collection of data. Three behavioural states were recorded: position (lying, standing, walking), oral activity (eating, ruminating, drinking) and attitude (tense, alert, resting, sleeping). When a full set of data had been collected the data set from a

single animal was collated and sorted by time of observation. The number of times each activity occurred during an observation hour was calculated and expressed as a percentage of the total number of observations in that hour. The mean number of minutes per hour spent in that activity was then calculated from the percentage value.

Where possible, all daytime observations were made in the first week of the study period. Night-time observations were carried out during a week when there was sufficient moonlight to make the observations. Night-time observation of donkeys with 8- and 11-hour access to rangeland was not necessary as these animals were kraaled during the hours of darkness and, therefore, could not exhibit any feed related activity. All cattle were observed at night so that ruminating activity could be recorded. Behavioural data was derived from mean values obtained from 3 composite 24-hour periods as described in Chapter 5.

Night-time observations proved problematic in the case of donkeys with 24-hour access to rangeland, as the group tended to disperse into the bush. Locating these animals was difficult and disrupted the observation schedule for the cattle. The IPERD bite meter proved more effective than manual observation in collecting night-time data from donkeys.

Focal observations

Focal observations were carried out in week one and three of ZP1 and ZP2. During each of these periods, data were collected over a 5-day period. The observations consisted of recording the number of steps and bites that occurred in a 5-minute observation period. The data were collected by trained observers equipped with 2

hand-held tally counters, a countdown timer and a notebook. Focal observations were only recorded when animals were actively foraging.

Focal observations were carried out at 06:00 h (24-hour and 11-hour access only), 08:00 h, 10:00 h, 12:00 h (8-hour treatment access only), 14:00 h, 15:00 h and 17:00 h (24-hour and 11-hour treatment access only). Observers were assigned 4 animals from one treatment group. During each observation session, the observer followed each animal in turn at a distance of 5-10 m for a period of 5 minutes. The groups were assigned to a different observer each day to reduce observer error, and animals were observed in a different sequence each day in order to balance the effect of diurnal variation.

During each 5-minute observation session, the observer would count, with the aid of 2 tally counters, each time the animal took a step forward and the number of bites taken. A bite was defined as the actual prehension and removal of material from a plant. Chews and exploratory mouth movements were not counted. In order to eliminate double counting a step was defined as the movement of the right foreleg off the ground, resulting in the animal moving forward; fidgeting or pest-related movements of the right foreleg were not counted.

The number of bites and steps taken in each 5-minute observation session was used to calculate bite and step rate per minute. The number of bites taken per step was used as a measure of the number of bites taken per feeding station, which has been suggested as a valuable indicator of the degree of selectivity practised by herbivores, particularly where feed supply is limited (Ruyle and Dwyer, 1985).

Animals were allowed to proceed to their chosen feeding site and settle to begin grazing before observation began. If an animal was not eating during its assigned observation session the next animal in the sequence was observed. If the animal commenced eating before the end of the observation session it was then observed for 5 minutes; if it did not then its step and bite rates were recorded as zero.

Rumination rates

Cattle were observed in the evenings between 16:00 h and 18:00 h on 3 successive evenings during each study period, and the number of rumination chews and the number of boli chewed were recorded over a 5-minute period. Average rumination rates and number of boli chewed in a minute were calculated.

Bite meter observations

The INRA bite meters were fitted to both cattle and donkeys during each study period. The ability of the equipment to distinguish between rumination and eating was questionable (see Chapter 3). For data collection purposes, the equipment was only used to provide additional data on night-time activity, because it became apparent from manual observations that cattle with 24-hour access to grazing did not forage during night-time hours, and all jaw movement during the night could be attributed to rumination. With donkeys, bite meters were only used to collect data from those with 24-hour access to grazing, as these animals wandered away from the observation area and could not be followed.

At the start of the 3-night observation period bite meter head-harnesses were fitted to 4 animals at 08:00 h of the morning of the observation period, and a dummy bite meter inserted into the carrying pouch. At 16:00 h the dummy bite meter was

replaced with a bite meter datalogger, and data were recorded through the night. The datalogger was removed at 08:00 h the following day and replaced with the dummy. The datalogger was then downloaded to a computer and the data checked to see if a successful recording had been made. This process was repeated on the following 2 evening and mornings, so that 3 complete sets of observations were obtained. Frequently the data collected was either incomplete or inaccurate (e.g. activity rates were lower than expected). In this case, observation of a particular animal was repeated until 3 whole nights of data had been collected.

Pest-related activity, such as head swinging, of kraaled animals was high, especially in the early evenings when biting flies were swarming around the animals. This activity increased the frequency of 'false bites' recorded by the bite meters. This activity often interrupted the consistency of rumination bouts, making it difficult for the INRA bite meter program to pick up rumination in the early evening. The problem was overcome to some degree by increasing the data filtering so that short bursts of oral activity were not misinterpreted as eating, and also by increasing the acceptable coefficient of variation for rumination bouts, so there was a wider tolerance for rumination behaviour. In practice, each file could be run through the program and the filters and tolerances adjusted until the amount of eating that was recorded was almost zero, but the level of rumination remained high.

8.3: Results

8.3.1: Climate

Results from the climatic monitoring are shown in Figures 8.1-8.4. Mean minimum temperatures were slightly higher in ZP1 (15.3°C) than in ZP2 (14.1°C). Mean

maximum temperatures were considerable higher during ZP1 (32.8°C) than in ZP2 (27.3°C). Mean maximum and minimum relative humidities were considerably higher during ZP2 (91.8% and 42.2% respectively) than during ZP1 (70.0% and 19.5% respectively). A climograph (Figure 8.3) was constructed from median daily values of temperature and relative humidity. To remove the effects of rain-showers on relative humidity and temperature, climograph data were trimmed by ranking each data set by relative humidity then removing the top and bottom 3 values. The climograph showed that ZP1 occurred during warmer, less humid conditions than ZP2. However, mean daily climatic conditions during both ZP1 and ZP2 did not approach those at which an effect on DMI would have been expected (Mount, 1979).

Little rain fell during either ZP1 or ZP2 (Figure 8.4); there was a total of 6 showers in ZP1 and 7 in ZP2. Most of this rain fell during the night, apart from one heavy shower (11 mm) during the cattle behavioural observation week in ZP1.

The general absence of rain during the 2 study periods was helpful since animals tend to stop eating during heavy showers so unrepresentative behavioural data are obtained.

Figure 8.1: Minimum and maximum temperatures (°C)showing seven day rolling average (---) at Matopos, Zimbabwe, October - November, 1996 and January - March 1997

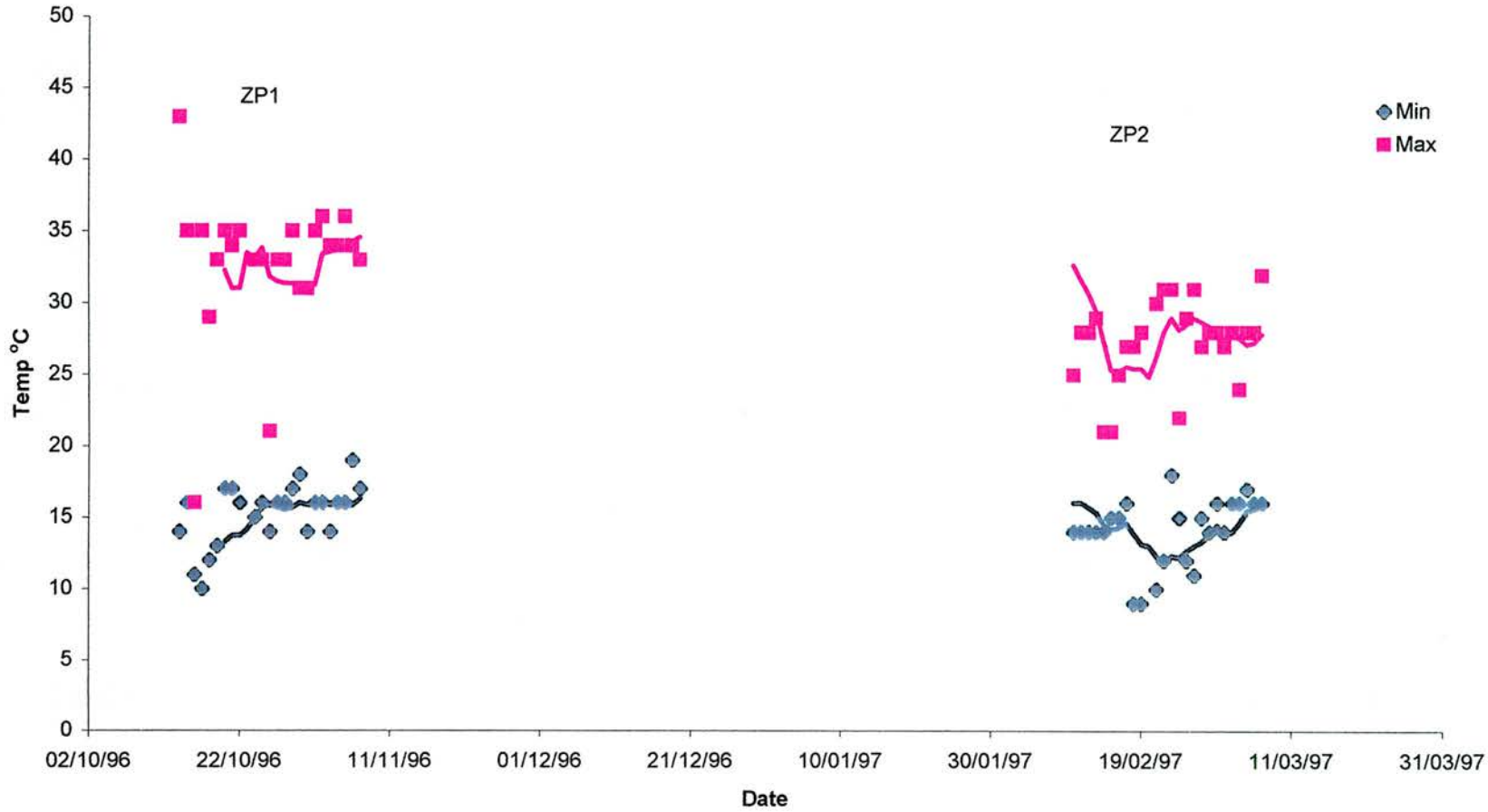


Figure 8.2: Minimum and maximum relative humidity showing seven day rolling average (---) at Matopos, Zimbabwe, October - November, 1996 and January - March 1997

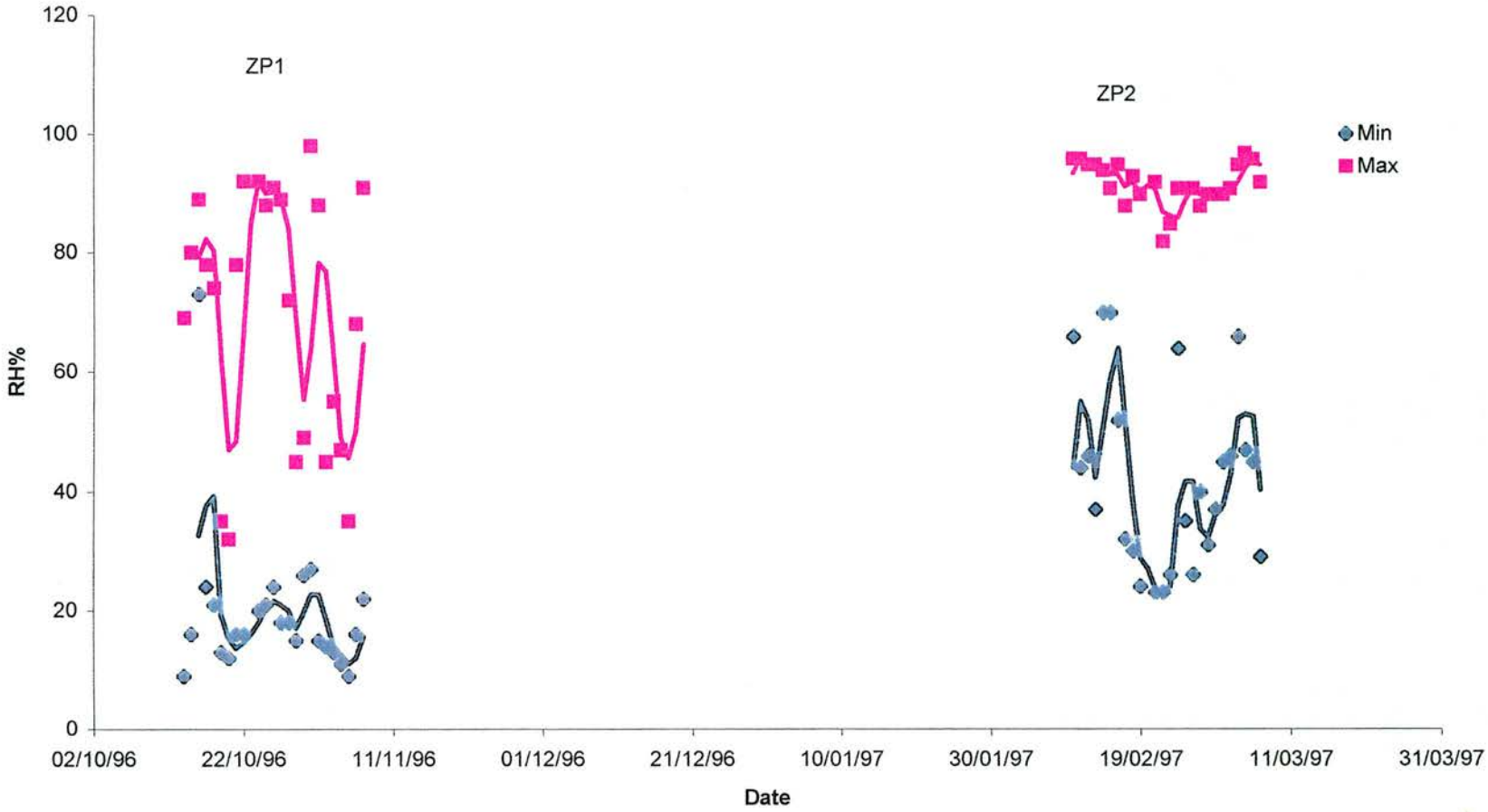


Figure 8.3 Climograph constructed from trimmed ambient climate data gathered at pasture during the dry (ZP1) and wet seasons (ZP2) at Matopos, Zimbabwe

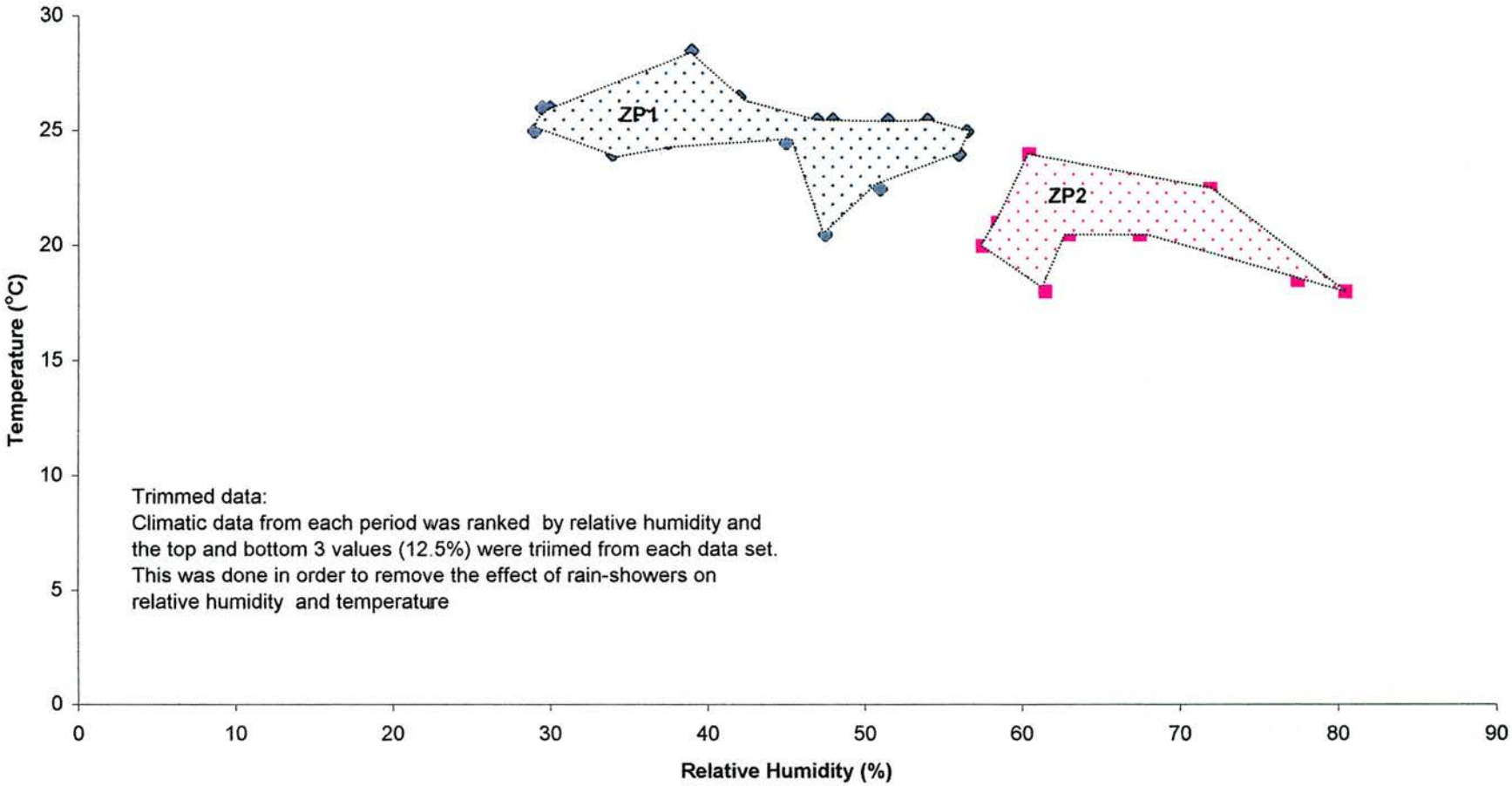
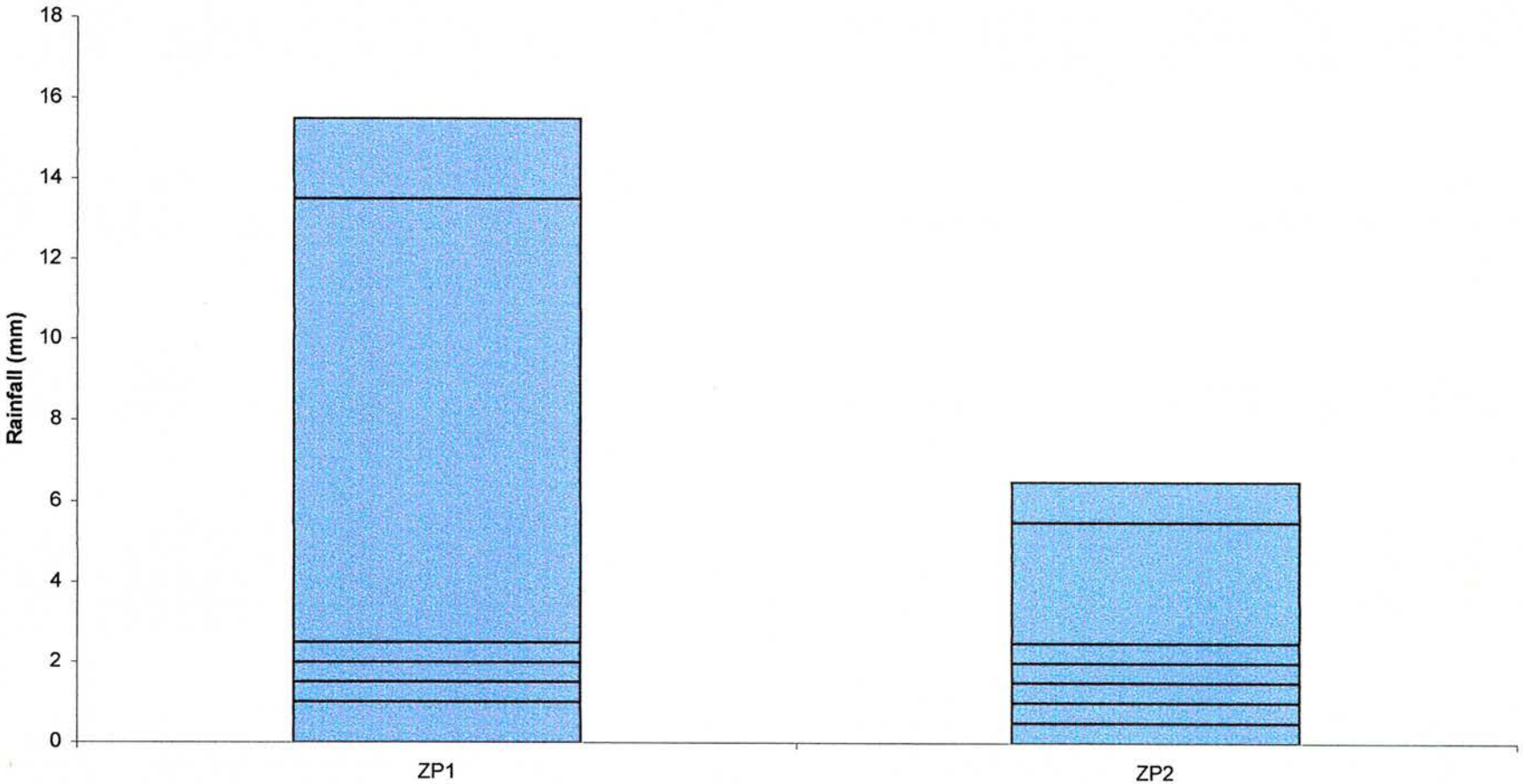


Figure 8.4 Cumulative rainfall during ZP1 and ZP2 showing the number of rainy days that contribution to total (bands within bars)



8.3.2: *Forage species occurring in the study area*

A total of 62 species of forage plants were collected from the study site (Table 8.2). Of these there were 21 species of dicotyledenous plant, 20 browse species and only one (*Solanum incnum*) was a forb. There were 41 species of grass collected from the site, the relative abundance of each species varying according to soil type and micro-ecological conditions. A detailed survey of the botanical composition of the study area was not possible because of its large area and the difficulty in obtaining an accurate ground plan of the site. It was also felt that the botanical composition of the site would not necessarily bear any relationship to the species that the animals selected to eat. As the project was principally involved with the value of the study area as a feed resource then the effort required to survey the study site was considered to be unjustified and irrelevant to the purpose of the work.

8.3.3: *Sward conditions*

Sward conditions during ZP1 and ZP2 were considerably different, in terms of sward quality but similar in terms of dry herbage mass (Table 8.2). The major nutritional differences between the 2 study periods were in terms of crude protein and hemicellulose.

The nutritional values of sward samples taken during ZP2 were greater than those taken during ZP1 (Table 8.3). During both experimental periods, all animals selected diets from the sward that that were of greater nutritional value than obtained with random sampling. The nutritional value of dietary samples taken for donkeys was greater than that for cattle in all cases. The dry herbage mass was similar in ZP1 and ZP2. However, fresh herbage mass was ~2.5 times greater during ZP2. Sward height and bulk density were not measured.

Table 8.2: Species of grass, browse and forb recorded at the study site

Dicotyledonous species	***Grass species*** (cont.)
Browse species	*Chloris virgata*
Acacia gerradii	*Cymbopogon caesius*
Acacia Karroo	*Cymbopogon plurinodis*
Acacia rehmanniana	*Cynodon dactylon*
Combretum hereroense	*Dichanthium papillosum*
Combretum imberbe	*Digitaria milanjiana*
Dichrostachys cineria	*Digitaria pentzii*
Disospyros lyciodes	*Eleusine indica*
Erhitia rigida	*Enneapogan cenchroides*
Euclea divinorum	*Eragrostis rigidior*
Euclea undulata	*Eragrostis superba*
Grewia monticola	*Eragrostis violacea de winter*
Grewia ternunervis	*Eragrostis viscose*
Ormacarpum trichorpum	*Heteropogon contortus*
Peltophorum africanum	*Hyparrhenia filipendula*
Proasparagus africanus	*Hyperthelia dissoluta*
Rhus pyroides	*Ischaemum afrum*
Rhus ternunervis	*Loudetia simplex*
Securinega virosa	*Panicum maximum*
Tarchonanthus camphoratus	*Pennisetum clandestinum*
Zizphus mucronata	*Perotis patens*
	Pogonarthria squarrosa
Forb species	*Rhynchelytrum nerviglume*
Solanum incnum	*Rottboellia exaltata*
	Schizachyrium sanguineum
Grass species	*Setaria anceps*
Andropoga gayanus	*Setaria incrasata*
Aristida barbicollis	*Sporobolus iocladas*
Aristida graciliflora	*Sporobolus pyramidalis*
Aristida meridionalis	*Themeda triandra*
Bothriochloa insculpta	*Trachypogon spicatus*
Brachiaria eruciformis	*Tricholaena monachne*
Cenchrus ciliaris	*Urochloa mosambicensis*
Chloris gayana	

Table 8.3: Mean herbage masses, dry matter and nutrient content (±s.e.) of quadrats sampled during ZP1 and ZP2 (units are g/kg DM unless stated).

	ZP1		ZP2	
Sampling phase relative to intake study	Pre	Post	Pre	Pre
Fresh Herbage Mass (g/m^2)	170 (16.2)	149 (8.1)	504 (39.8)	290 (11)
Dry Herbage Mass (g/m^2)	155 (14.6)	142 (7.7)	159 (7.1)	134 (5.6)
Dry Matter (g/kg)	914 (14.6)	952 (3.0)	335 (14.0)	465 (14.0)
Organic Matter	908 (4.8)	902 (4.8)	888 (7.4)	902 (5.9)
Neutral Detergent Fibre	875 (22.2)	884 (3.8)	920 (5.7)	905 (4.9)
Acid Detergent Fibre	523 (8.2)	511 (7.1)	490 (7.6)	481 (7.7)
Acid Detergent Lignin	85 (4.8)	86 (2.3)	82 (4.7)	83 (8.0)
Crude Protein	31 (1.3)	33 (1.2)	68 (3.1)	54 (2.2)

8.3.4: Live weight

Live weight changes occurring in donkeys and cattle during ZP1 and ZP2 are shown in Figures 8.5 and 8.6; there were no significant differences during either of the study periods for both species. In both cattle and donkeys, the live weight of the groups with 24-hour and 8-hour access became increasingly divergent; with the live weights of the 11-hour access being intermediary between the other 2 during ZP2.

Differences in live-weight changes between ZP1 and ZP2 were significant ($P<0.001$) for both cattle and donkeys. Cattle and donkeys lost weight during ZP1 (-10.0 kg and –1.5 kg respectively) and gained weight during ZP2 (36 kg and 7.7 kg respectively).

8.3.5: Faecal recovery of external markers

Estimated FO using either Cr_2O_3 or C_{36} alkane as external markers were significantly different ($P<0.01$) from the measured value when the group of 24 animals was considered as a whole (Table 8.4). In the case of Cr_2O_3, when the cattle and donkey groups were analysed separately, the differences between measured and estimated FO were smaller but still significantly different ($P<0.05$). The difference between measured and estimated FO using C_{36} alkane was not significant in the case of the donkeys, but significant in the case of cattle ($P<0.05$).

The Cr_2O_3 marker under-estimated FO relative to the measured values (mean difference between measured and estimated -0.31 kg) whilst the C_{36} alkane consistently over-estimated values relative to measured FO (mean difference between measured and estimated +0.26 kg).

Figure 8.5: Effect of access time to grazing on the live weight of donkeys between October, 1996 and March 1997

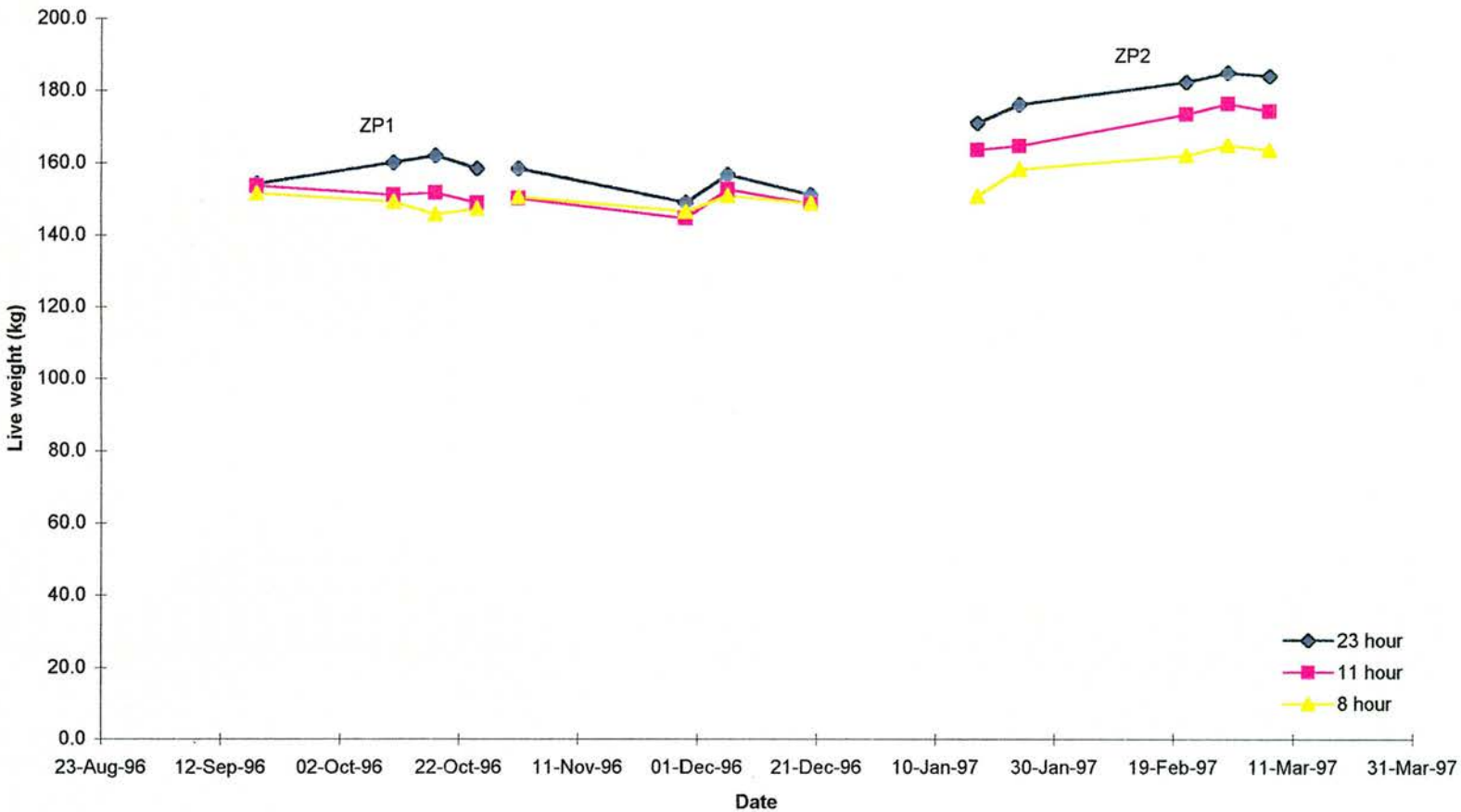


Figure 8.6 Effect of access time to grazing on live weight of cattle between October, 1996 and March 1997

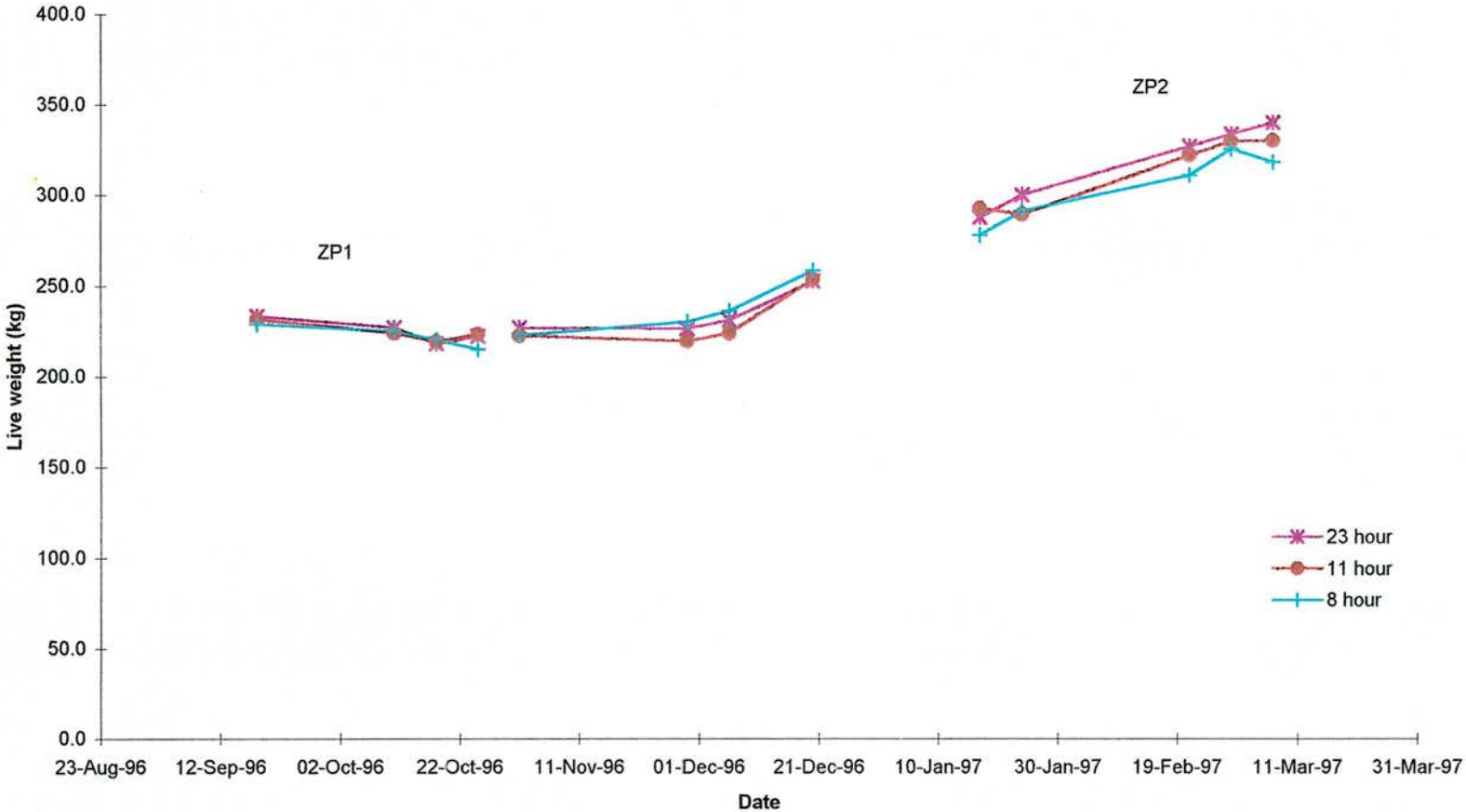


Table 8.4 Comparison between measured faecal outputs (kg day^{-1} DM) (± s.e) and estimated faecal outputs (kg day^{-1} DM) (± s.e) using Cr_2O_3 or C_{36} alkane external markers in cattle and donkeys.

		Faecal output		
	n	Measured	Cr_2O_3	C_{36}
Donkeys	12	1.31 (0.225)	0.95 (0.226)	1.51 (0.265)
Cattle	12	1.58 (0.081)	1.31 (0.121)	1.89 (0.147)
All animals	24	1.44 (0.135)	1.13 (0.150)	1.70 (0.171)

The recovery values for the 2 external markers are shown in Table 8.5. There was no significant difference between donkeys and cattle in the recovery of C_{36} alkane marker. However, there was a significant difference ($P<0.01$) between donkeys and cattle in the recovery of the Cr_2O_3 marker.

Table 8.5 Comparison between faecal recoveries (%) (±s.e.) of Cr_2O_3 and C_{36} alkane external markers in cattle and donkeys.

		Faecal recovery	
	n	Cr_2O_3	C_{36}
Donkeys	12	137.3 (13.4)	93.2 (7.3)
Cattle	12	115.5 (7.4)	91.3 (5.6)
All animals	24	126.4 (8.7)	92.2 (4.5)

Estimated FO that had been corrected for incomplete recoveries were closer to the measured FO than the uncorrected FO (Table 8.6). For donkeys, there were no significant differences between the measured FO and the estimated FO using either

marker. For cattle, the differences between measured FO and estimated FO were significant for both markers. The differences were more significant for the Cr_2O_3 marker ($P<0.01$), than for C_{36} alkane marker ($P<0.05$).

Table 8.6 Comparison between measured and corrected estimated faecal outputs (kg day^{-1} DM) (± mean residual) using Cr_2O_3 or C_{36} alkane external markers in cattle and donkeys.

			Corrected faecal output	
	n	Measured	Cr_2O_3	C_{36}
Donkeys	12	1.31	1.38 (0.20)	1.41 (0.17)
Cattle	12	1.58	1.90 (0.33)	1.76 (0.21)
All animals	24	1.44	1.64 (0.27)	1.58 (0.19)

From the analysis of faecal recoveries of the 2 external markers it was apparent that C_{36} marker gave the most reliable estimation of FO. Subsequent DMI estimates were, therefore, based on FO calculated from corrected C_{36} faecal concentrations.

8.3.6: Dry matter intake

Forage DMI estimated using alkane pair (ALK), double marker (DMA) or external marker *in vitro* DMD (EM-IV) methods for cattle and donkeys during ZP1 and ZP2 are shown in Figure 8.7. Overall statistical analysis (ANOVA) of the 3 methods showed that there was no significant difference between the DMA method and the other 2, but there was a significant ($P<0.01$) difference between the ALK and EM-IV methods.

Figure 8.7: Estimates of daily DMI (+/- s.e.) using alkane pairs (Alk), internal and external markers (DMA) and external marker with *in vitro* dry matter digestibility (EM-IV) methods in cattle and donkeys during dry season (ZP1) and wet season (ZP2)

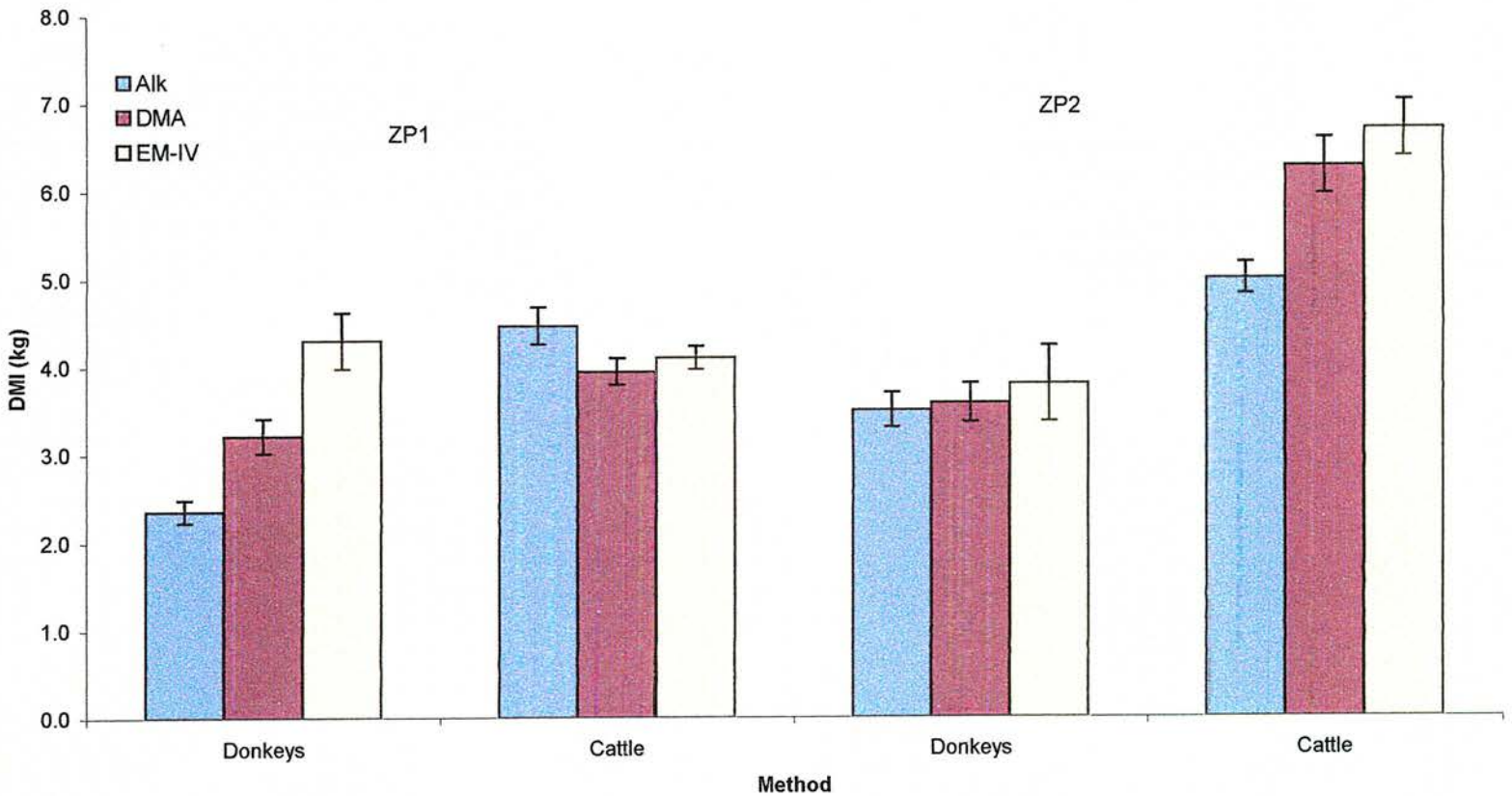


Table 8.7: Mean concentration and coefficient of variation (%) of C_{35} alkane (mg/kg DM) and ADL (g/kg DM) internal markers in dietary and faecal samples gathered from donkeys and cattle during two grazing studies in Zimbabwe.

	C_{35} in diet		C_{35} in faeces		ADL in diet		ADL in faeces	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
ZP1								
Cattle	15.1	78.7	41.4	12.5	50.1	39.2	106.0	12.2
Donkeys	18.6	63.6	40.7	32.2	47.7	23.0	126.0	10.0
ZP2								
Cattle	40.7	24.7	63.2	28.0	90.1	8.1	162.4	7.8
Donkeys	30.5	52.3	76.2	22.0	73.0	13.7	122.0	6.7

The daily DMI estimated by the 3 methods showed significant differences from each other in donkeys during ZP1 (ALK vs. DMA, $P<0.01$; ALK vs. EM-IV, $P<0.001$; DMA vs. EM-IV, P.0.05). In cattle during ZP2 there were significant differences between the ALK method and the other 2 methods (ALK vs. DM, $P<0.01$; ALK vs. EM-IV, $P<0.001$).

The reliability of the DMI estimate using the ALK method is questionable because of the low alkane concentration of the plant material (Table 8.7). The concentrations of dietary C_{35} alkanes, which formed part of the alkane pair used to estimate DMI, were very low (mean 26.2 mg/kg DM), particularly during ZP1 (16.9 mg / kg DM). The reliability of the ALK method diminishes as the concentration of alkane in the sample decreases, (R.W. Mayes, MLURI, Aberdeen, Scotland; personal communication) because the analytical error has a greater effect on the outcome of the DMI calculation. Estimates of DMI with the ALK and EM-IV methods were most similar

when the C_{35} alkane concentration of the dietary samples were highest, for example in donkeys during ZP2.

As there were only small differences between estimates of DMI obtained using the EM-IV or DMA (only reaching significant levels in donkeys during ZP1) mean value of the 2 methods were taken. Estimated DMI for donkeys and cattle in the 3-treatment groups during ZP1 and ZP2 using the mean value from the EM-IV and DMA methods are shown in Table 8.8 and Figure 8.7.

Table 8.8: Estimated dry matter intake per unit of metabolic live weight (g per $kg^{0.75}$ per day) (± s.e.) by cattle and donkeys in the three treatment groups during ZP1 and ZP2, using the mean value obtained by the EM-IV and DMA methods.

Rangeland access	23 hour	11 hour	8 hour	Species/Period mean
ZP1				
Cattle	69 (5.9)^{k}	77 (0.7)^{l}	65 (1.9)^{m}	70 (2.4)^{d}
Donkeys	90 (5.5)^{ab}	66 (3.4)^{a}	65 (5.4)^{b}	74 (6.9)^{c}
ZP2				
Cattle	93 (6.0)^{k}	99 (7.5)^{g,l}	80 (6.2)^{g,m}	91 (4.2)^{f,d}
Donkeys	85 (2.9)^{h,i}	70 (6.0)^{h}	66 (3.2)^{i}	80 (3.7)^{fc}

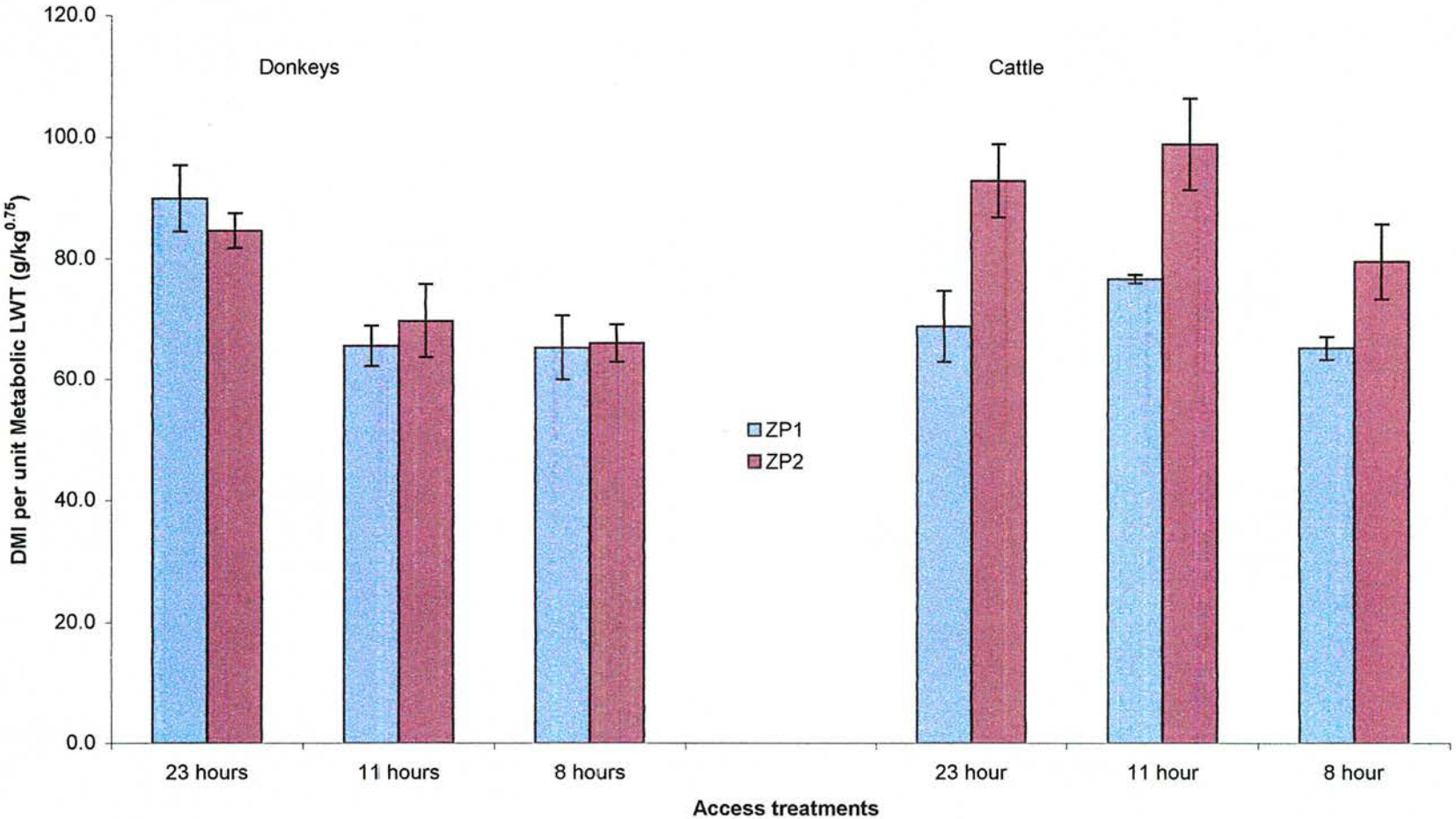
d,f,m Values that share the same superscript differ significantly ($P < 0.05$).
g,h,k,l Values that share the same superscript differ significantly ($P < 0.01$).
a,b,c,e,i,j Values that share the same superscript differ significantly ($P < 0.001$).

Overall, there were no significant differences between the DMI ($g/kg^{0.75}$) of cattle and donkeys. However, during ZP2 cattle had a significantly higher value ($P<0.05$) than donkeys had. This difference between species masked the effect of season on DMI,

which overall was not significant. However there were highly significant seasonal effects if the data were analysed by species (Table 8.8 and Figure 8.8).

During ZP1, donkeys with 23-hour access to grazing ate significantly more ($P<0.001$) than donkeys in the other groups. There was no significant difference between the DMI of donkeys grazing for 11 hours compared to those with 8-hour access, despite the latter group eating consistently more than the former. During ZP2, there was no significant difference between the DMI of donkeys grazing for 23 hours compared to those with 11-hour access. However, during ZP2 the donkeys with 8-hour access ate significantly less than either the 23- ($P<0.001$) or the 11-hour access group ($P<0.01$).

Figure 8.8: Daily dry matter intake per unit of metabolic live weight (g/kg$^{0.75}$) with s.e.of three treatment groups of cattle and donkeys during dry season (ZP1) and wet season (ZP2)



In cattle, access time generally had less effect on DMI than in donkeys. During ZP1, there were no significant differences between treatments, and in ZP2 the only significant difference between treatments occurred between the 11- and 8-hour access groups ($P<0.01$).

8.3.7: Diet quality

Comparison of QI values of diets showed that donkeys selected a diet that was of significantly higher quality ($P<0.001$) than that selected by the cattle. This difference was most evident in terms of CP content, ADF content and IV-DMD of the selected diets, particularly during ZP1 (Table 8.9). The QI values of selected diets were significantly greater ($P<0.001$) during ZP2 than during ZP1, reflecting the better quality of available forage during ZP2 (Table 8.9).

Overall, there was no effect of access to rangeland on the quality of the diet selected, however, significant effects did become apparent when the data were analysed by season and by species. There were no significant effects of treatment during ZP2, when feed quality was much higher than during ZP1. During ZP1, cattle with 24-hour access to grazing selected a diet that had significantly higher QI values ($P<0.01$) than that selected by cattle with only 11- or 8-hour access; the diet was higher in both CP and IV-DM with lower levels of NDF and ADF. In donkeys there was a significant difference in QI ($P<0.01$) only between the 24- and 8-hour treatments.

Table 8.9: Neutral-detergent fibre (NDF) (g/kg DM), acid-detergent fibre (ADF) (g/kg DM), crude protein (CP) (g/kg DM), *in vitro* dry matter digestibility (IV-DMD) (proportion in DM) and quality index (QI) of hand-plucked representative samples of forage eaten by donkeys and cattle during ZP1 and ZP2 (±s.e.).

Rangeland access	23 hour	11 hour	8 hour	Species/Period mean
ZP1				
Cattle				
NDF	719 (7.6)	743 (10.1)	742 (3.0)	731 (16.4)
ADF	454 (5.7)	471 (5.1)	461 (36.8)	457 (14.1)
CP	52 (1.7)	46 (2.1)	47 (1.1)	49 (1.1)
IV-DMD	0.47 (-)	0.45 (-)	0.46 (-)	0.45 (-)
QI	34 (1.5)[a,b]	28 (1.6)[a]	29 (0.6)[b]	32 (1.0)[c,d]
Donkeys				
NDF	704 (6.1)	721 (5.1)	737 (4.1)	720 (3.4)
ADF	427 (6.2)	423 (5.6)	419 (5.1)	720 (5.7)
CP	63 (0.3)	62 (0.9)	61 (1.6)	62 (3.2)
IV-DMD	0.54 (-)	0.53 (-)	0.52 (-)	0.53 (-)
QI	48 (0.5)[e]	45 (1.0)	43 (1.3)[e]	45 (1.0)[c,f]
ZP2				
Cattle				
NDF	728 (4.9)	730 (5.5)	735 (4.5)	731 (9.5)
ADF	330 (22.7)	255 (13.6)	309 (32.9)	298 (15.9)
CP	75 (0.9)	78 (1.7)	75 (1.6)	76 (0.9)
IV-DMD	0.61 (-)	0.63 (-)	0.63 (-)	0.62 (-)
QI	63 (0.8)	67 (1.8)	65 (1.6)	65 (0.9)[dg]
Donkeys				
NDF	736 (2.3)	724 (5.5)	730 (3.8)	730 (2.5)
ADF	349 (3.5)	342 (7.6)	329 (11.7)	340 (5.0)
CP	89 (1.2)	89 (0.8)	90 (3.0)	90 (1.0)
IV-DMD	0.64 (-)	0.63 (-)	0.64 (-)	0.64 (-)
QI	78 (1.2)	76 (0.8)	79 (2.7)	78 (1.0)[f,g]

[a,b,e] Values that share the same superscript differ significantly ($P < 0.01$).

[c,d,f,g] Values that share the same superscript differ significantly ($P < 0.001$).

8.3.8: Time spent eating and ruminating

Overall, donkeys spent significantly ($P<0.001$) more time eating than did cattle (Table 8.10). Only during ZP2, when time of access to grazing was limited to 8 hours were there no significant differences in time spent eating between cattle and donkeys.

Overall, significantly ($P<0.001$) more time was spent eating during ZP2 than during ZP1. In all the cattle treatment groups, animals spent significantly more time eating during ZP2 than in ZP1. However, only the donkeys with 24-hour access to grazing spent significantly more time eating in ZP2 than in ZP1 (Table 8.10).

Access time to rangeland had a large effect on the amount of time spent eating. Overall, there were significant differences ($P<0.001$) between all 3 treatments; time spent eating increasing with the access time to grazing. The effects of treatments were more pronounced in donkeys than cattle (Table 8.10). In cattle, during ZP1 the access time had a greater effect on time spent eating than during ZP2.

There were significant differences ($P<0.001$) between time spent ruminating by cattle during ZP1 and ZP2. The only significant effects of access time occurred during ZP2, when cattle with 24-hour access to grazing spent significantly ($P<0.05$) more time ruminating than cattle in either of the other 2 groups.

Table 8.10 Mean time spent eating, ruminating and total feed related oral activity (minutes) in cattle and mean time spent eating (minutes) in donkeys during ZP1 and ZP2 (±s.e.)

Rangeland access	23 hour	11 hour	8 hour
Cattle			
ZP1			
Eating	593 (2.3)^{a,b,m,t}	539 (1.9)^{a,c,n,u}	402 (1.3)^{b,c,o,v}
Ruminating	311 (15.5)	323 (16.7)	317 (21.4)
Total	904 (15.6)	862 (18.4)	719 (21.0)
ZP2			
Eating	637 (19.8)^{g,h,p,t}	593 (7.8)^{g,i,q,u}	442 (2.3)^{i,h,v}
Ruminating	495 (32.4)^{r,s,w}	437 (19.8)^{r}	456 (17.5)^{s}
Total	1132 (21.1)	1030 (21.8)	898 (17.0)
Donkeys			
ZP1			
Eating	814 (12.1)^{d,e,m,w}	679 (1.2)^{d,f,n}	458 (1.7)^{e,f,o}
ZP2			
Eating	1019 (38.5)^{j,k,p}	698 (1.5)^{j,l,q}	466 (1.0)^{k,l}

g,r,s,t Values that share the same superscript differ significantly ($P < 0.05$).

a,o,u,v Values that share the same superscript differ significantly ($P < 0.01$).

b,c,d,e,f,h,i,j,k,l,m,n,p,q,w Values that share the same superscript differ significantly ($P < 0.001$).

8.3.9: Circadian pattern of feeding and rumination behaviour

The treatments had little effect on ETPH during the common grazing hours (08:00 h - 16:00 h) except in cattle during ZP2 (Figures 8.9 – 8.12).

In cattle during ZP1 there was little difference in ETPH between treatment groups, the only exception was between 12:00h–13:00h (when cattle generally went to drink); the 8-hour group spent 10–14 minutes more per hour grazing during this period. This was achieved at the expense of time spent ruminating and idling at the water trough; actual time spent drinking was not affected (Table 8.11).

Figure 8.9: Time spent eating per hour by cattle given different access to rangeland during ZP1

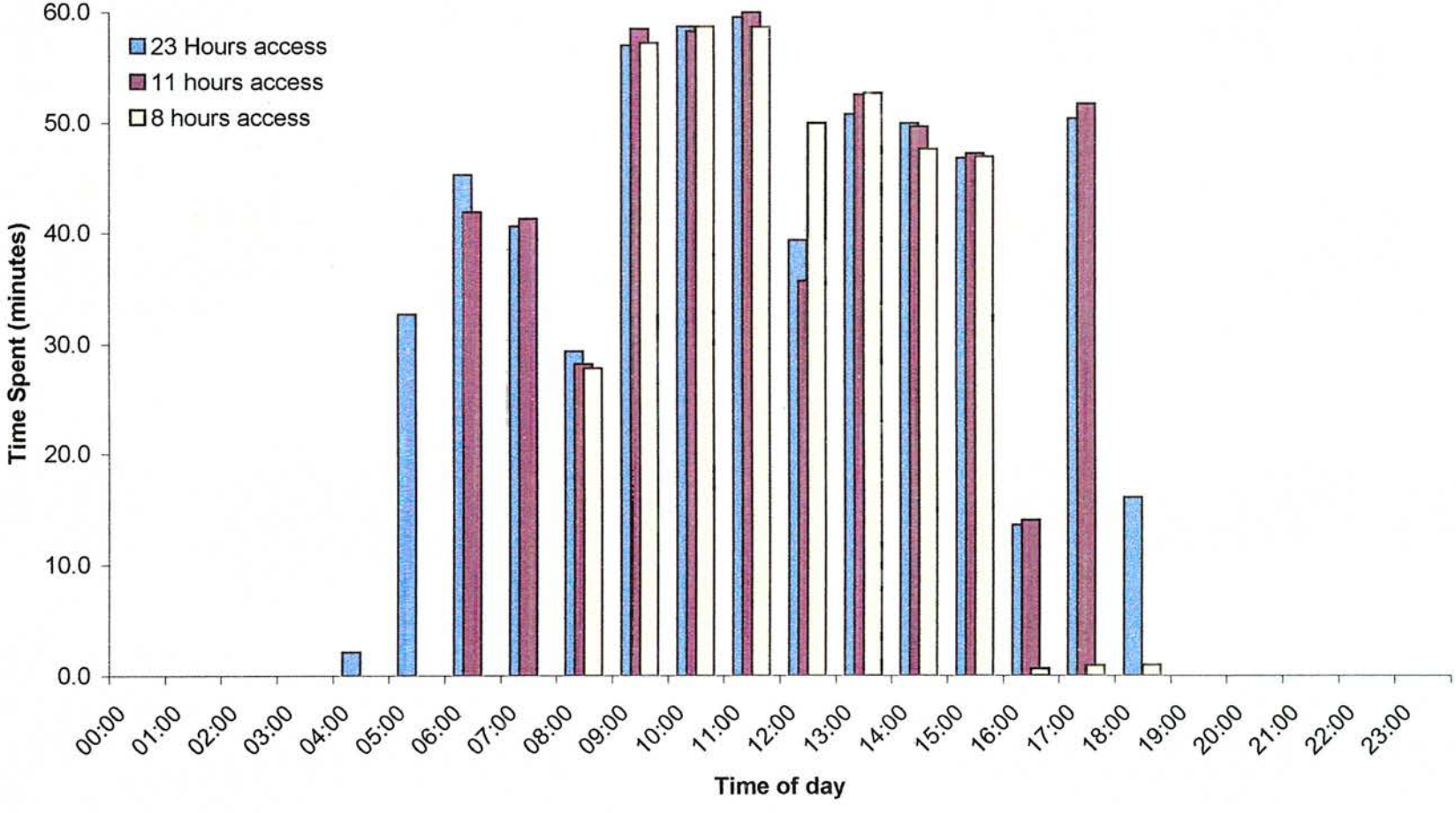


Figure 8.10: Time spent eating per hour by donkeys given different access to rangeland during ZP1

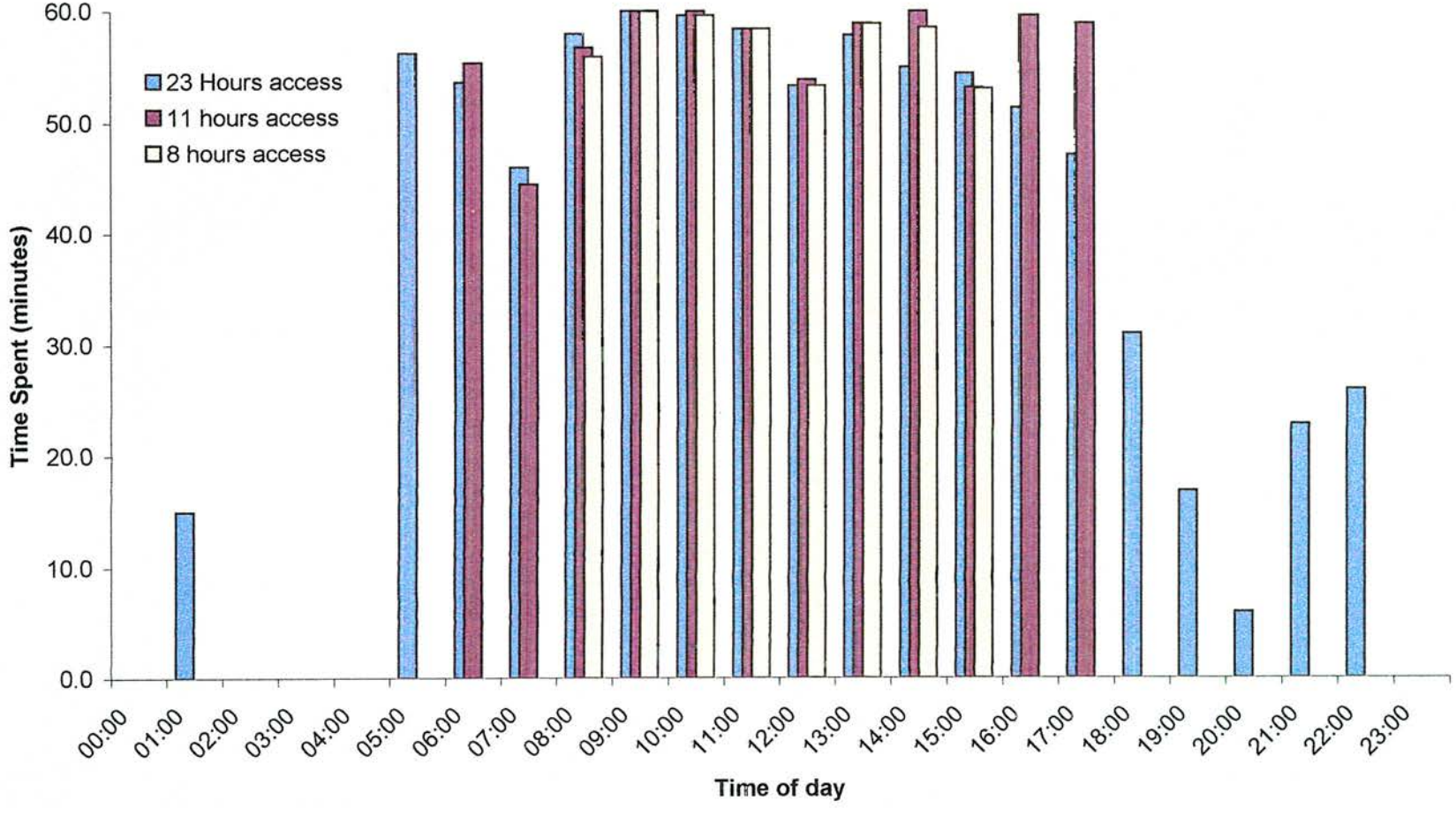


Figure 8.11: Time spent eating per hour by cattle given different access to rangeland during ZP2

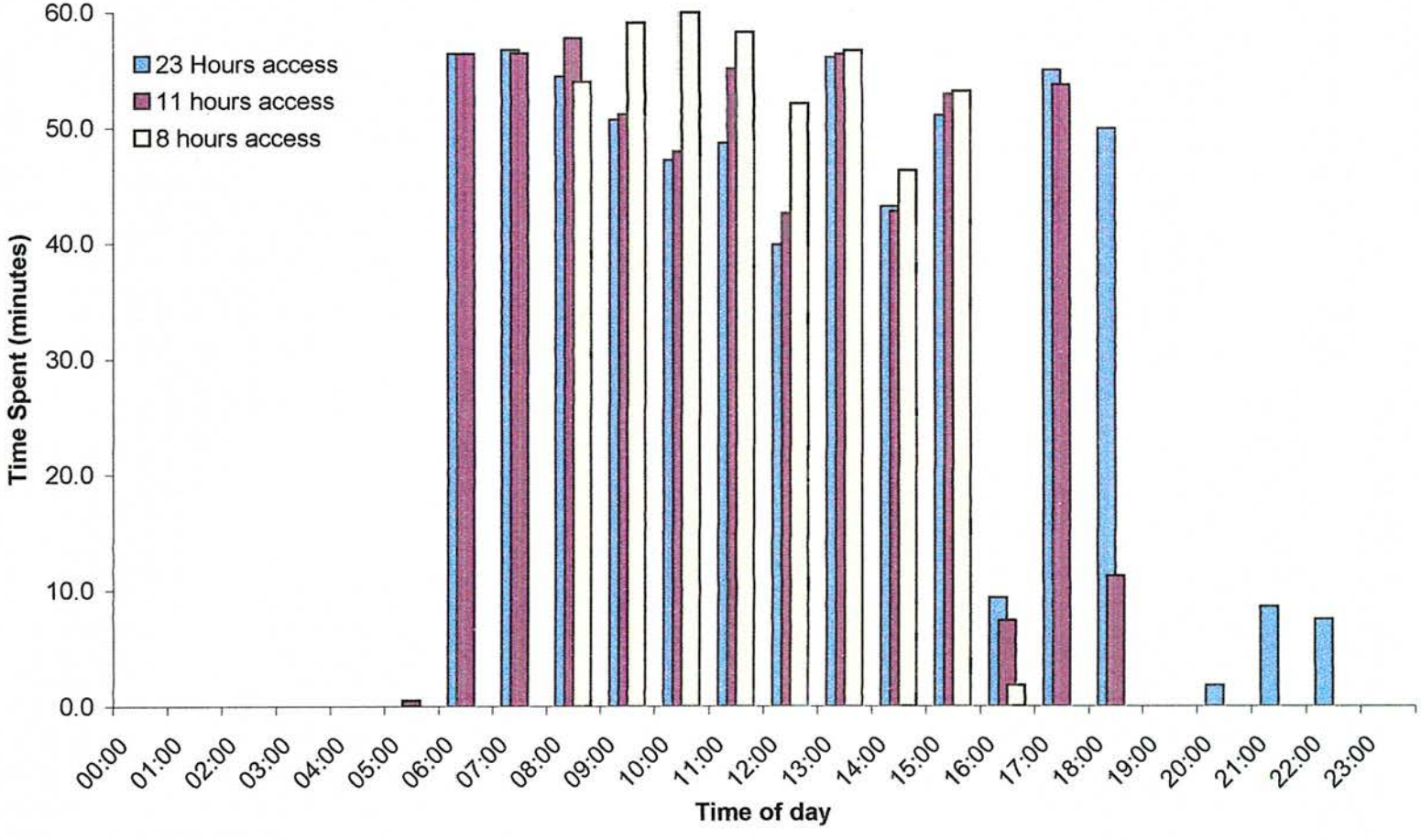
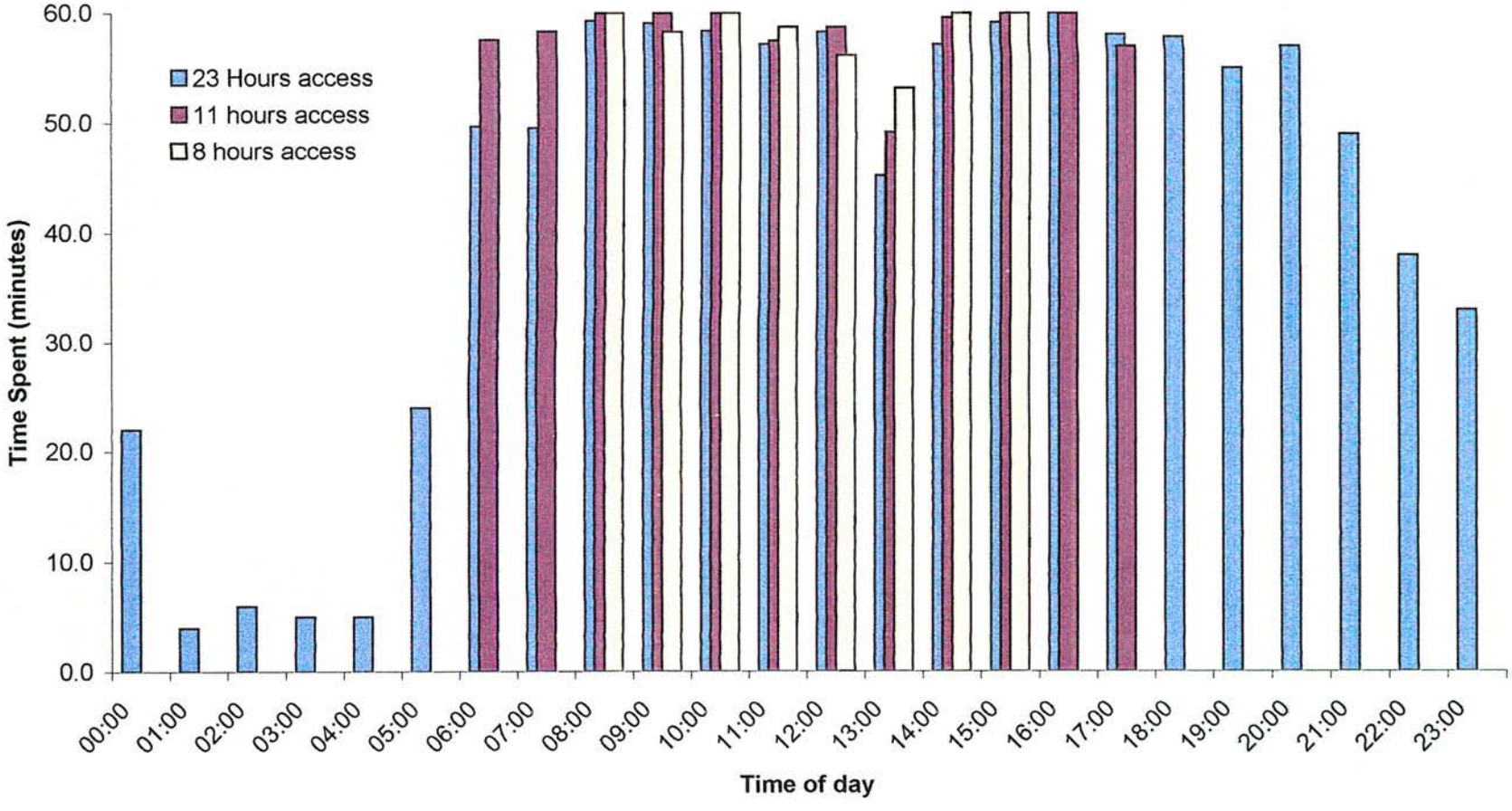


Figure 8.12: Time spent eating per hour by donkeys given different access to rangeland during ZP2



Drinking activity in cattle was highly synchronised within the herd, with all animals trekking to the water trough at around midday. Cattle with 8-hour access tended to leave the water trough area sooner than those in the other groups, often spending the remainder of their feeding time grazing separately from the main herd.

Drinking-related behaviour (i.e. trekking, drinking and idling by the trough) in cattle during ZP2 was less well defined, with animals making visits to the water trough at any time between 11:00h and 15:00h. The ETPH of the 8-hour access group was greater than for the other 2 groups for the greater part of the morning (Figure 8.10); this was achieved at the expense of time spent ruminating (Figure 8.14). The circadian patterns of ETPH of the groups with 24- and 11-hour access during common grazing hours were very similar to each other.

The cattle in the 24-hour access group were seldom observed to graze during the hours of darkness; that which did occur was only observed in a single animal on one occasion. Differences in the time spent grazing per day between the 11- and 24-hour groups occurred during the additional daylight hours available to the 24-hour group, either just after dawn or before dusk (Figures 8.9 and 8.10). Although the possibility that these cattle were exhibiting allelomimetic behaviour cannot be ruled out, it should be noted that cattle in this group were accustomed to having 24-hour access to rangeland for a period of 18–24 months before the grazing study began. Furthermore, although the 24-hour group returned to the kraal area at dusk and spent the night close to the cattle in the other groups, they left the kraal area to graze as soon as it got light.

Table 8.11: Time spent (minutes) eating, ruminating, drinking, idling and lying down(±s.e.) between 12:00h and 13:00h in cattle and donkeys during ZP1 and ZP2.

Rangeland access	24 hour	11 hour	8 hour
ZP1			
Cattle			
Eating	39 (3.0)	36 (1.0)	50 (0.5)
Ruminating	4 (1.7)	9 (1.3)	0 (0)
Drinking	2 (0.6)	2 (0.8)	2 (0.9)
Idling	14 (3.1)	14 (1.8)	8 (0.5)
Lying down	8 (2.2)	11 (1.1)	1.6 (0.5)
Donkeys			
Eating	53 (4.8)	54 (0.6)	54 (0.9)
Drinking	1 (-)	1 (-)	2 (-)
Idling	7 (4.8)	6 (0.6)	4 (0.6)
Lying down	0 (-)	0 (-)	0 (-)
ZP2			
Cattle			
Eating	40 (0.9)	43 (0.6)	52 (1.8)
Ruminating	9 (1.0)	8 (0.4)	3 (0.4)
Drinking	2 (0.4)	2 (-)	2 (-)
Idling	12 (1.4)	9 (0.9)	5 (1.5)
Lying down	8 (1.1)	5 (1.2)	0.5 (0.4)
Donkeys			
Eating	58 (-)	59 (0.4)	56 (0.5)
Drinking	2 (-)	1 (0.5)	2 (1.2)
Idling	0 (-)	1 (0.4)	2 (0.7)
Lying down	0 (-)	0 (-)	0 (-)

Between 12:00 h and 13:00 h appeared to be the time of day when cattle would naturally reduce grazing activity and rest (Table 8.11), possibly due to the high ambient temperatures (mean noon temperature - 32°C) and relative humidity (mean noon relative humidity 80%) during this period of the day. The frequency of lying down and idling in cattle with 8-hour access to grazing was significantly lower than that of the other 2 groups during the hour after noon ($P<0.001$).

The circadian patterns of feeding behaviour of each donkey group during the common grazing hours were very similar to each other (Figures 8.10 and 8.11). ETPH was rarely less than 50 minutes per hour, apart from when experimental procedures prevented access to grazing, for example, during dosing and when taking faecal grab samples. ETPH decreased between 12:00 h and 13:00 h, mainly due to the donkeys trekking to the water trough to drink. Donkeys did not generally graze as a herd, but tended to forage singly, as pairs or in small groups of between 3 and 5 animals. Despite this, drinking was highly synchronised, with all donkeys generally arriving at the water trough at the same time.

Donkeys with 24-hour access to grazing grazed during the night in contrast to cattle. Generally, these animals would graze until midnight, when they returned to the kraal area until dawn. Night grazing between dusk and midnight consisted of 2 distinct periods. There was a period of 2 to3 hours after dusk, when all other donkeys were confined in kraals, when donkeys with free access to grazing would graze close to the kraal. This was then followed by a 2 to3 hour feeding-foray beyond the immediate kraal area. Following the donkeys during these night-time forays was not possible because of the density of the bush and darkness; bite meter measurements were relied on to record feeding activity. The donkeys generally returned to the kraal around midnight. Night-time feeding-forays may have been related to moonlight, as all night observations where carried out when the moon was full.

8.3.10: Focal studies

Detailed statistical analysis of the effect of treatment on bite and step rate could not be carried out because there were insufficient replicates in each discrete data set to conduct non-parametric analysis. Non-parametric analysis (Mann-Whitney 'u' test)

was used to examine whether season or species had any effect on bite or step rate. Parametric analysis (ANOVA) was applied to all other focal data.

Bite rate (Table 8.12) in cattle was significantly higher ($P<0.001$) during ZP2 than during ZP1; the opposite was true for donkeys ($P<0.01$). Cattle also had a significantly higher ($P<0.001$) bite rate than donkeys, regardless of season. Step rate was significantly higher in cattle than in donkeys ($P<0.001$) and cattle had a significantly higher ($P<0.001$) step rate during the dry season (ZP1) than during the wet season. There was no significant effect of season on the step rate of donkeys.

There were no significant effects of season on the number of bites per day by donkeys. Cattle took significantly ($P<0.001$) more bites per day during ZP2 than ZP1, reflecting the overall greater DMI during this period. Donkeys made significantly ($P<0.001$) more bites per day than cattle during ZP1, but significantly less ($P<0.001$) during ZP2. Grazing access also had significant effects on bites per day (Table 8.12).

In cattle, there was no significant difference between the number of bites per day of the 24- and 11-hour groups, despite significant differences ($P<0.001$) in the time spent eating (Table 8.10). There were highly significant ($P<0.001$) differences in the number of bites per day between the 8-hour group and the other 2 groups.

In donkeys there were significant differences ($P<0.001$) in the number of bites per day between all treatments, with the number of bites increasing as more time was available for eating (Table 8.12). Donkeys with 24-hour access to grazing made significantly ($P<0.05$) more bites per day during ZP2 than ZP1, but the reverse was true for donkeys with 11-hour access (Table 8.12).

There was no significant effect of species on number of steps per day during ZP1 however, donkeys took significantly (P<0.01) more steps per day during ZP2 than cattle. There was no significant seasonal effect on the number of steps per day in donkeys, however cattle took significantly (P<0.01) more steps per day during ZP1 than during ZP2.

Table 8.12: Total number of bites and steps during rangeland access (±s.e.) in cattle and donkeys in three treatment groups during ZP1 and ZP2 given different access to rangeland

Rangeland access		24 hour	11 hour	8 hour
Bites per day				
Cattle	ZP1	12145 (396)^{a,k}	11732 (291)^{b,l}	9254 (188)^{a,b,m}
	ZP2	17006 (466)^{f,k}	17195 (526)^{g,l}	13214 (279)^{f,g,m}
Donkey	ZP1	17801 (797)^{c,e,n}	14951 (409)^{c,d,o}	10529 (160)^{e,d}
	ZP2	19513 (1142)^{h,i,n}	13432 (308)^{h,j,o}	10374 (220)^{i,j}
Steps per day				
Cattle	ZP1	4294 (139)^{p,y}	4043 (260)^{q,z}	2313 (97)^{p,q}
	ZP2	4257 (412)^{t,y}	3738 (200)^{u,z}	2403 (111)^{t,u}
Donkey	ZP1	3335 (127)^{r}	3413 (186)^{s}	2312 (106)^{r,s}
	ZP2	4386 (154)^{v,w}	3527 (179)^{v,x}	2484 (131)^{w,x}

n,o,z Values that share the same superscript differ significantly (P < 0.05).

a,b,v,y Values that share the same superscript differ significantly (P < 0.01).

c,d,e,f,g,h,I,j,k,l,m,p,q,r,s,t,u,w,x Values that share the same superscript differ significantly (P < 0.001)

All animals with 8-hour access to grazing took significantly (P<0.001) fewer steps per day than either of the other 2 groups during both ZP1 and ZP2 (Table 8.12). There were no significant differences between the number of steps per day taken by cattle with 24-hour access to grazing or those with 11–hour access. However, donkeys with 24-hour access to grazing took significantly (P<0.01) more steps per day than those with 11-hour access during ZP2 but not during ZP1 (Table 8.12)

Table 8.13: Bite rate (bites per minute), bites per step, bite size (g), bite size per unit of metabolic live weight (mg per $M^{0.75}$) and rate of intake (g per minute) in cattle and donkeys during ZP1 and ZP2 given different access to rangeland (± s.e.)

Rangeland access		24 hour	11 hour	8 hour
Bite rate				
Cattle	ZP1	20 (1.5)	22 (1.7)	22 (1.5)
	ZP2	25 (4.0)	28 (1.8)	29 (6.0)
Donkey	ZP1	22 (4.3)	23 (2.9)	26 (1.2)
	ZP2	17 (1.8)	20 (1.8)	22 (1.4)
Bites per step				
Cattle	ZP1	3 (0.2)^{a,c}	3 (0.2)^{b,d}	4 (0.2)^{a,b,e}
	ZP2	4 (0.3)	4 (0.2)	5 (0.3)
Donkey	ZP1	5 (0.2)^{c}	5 (0.2)^{d}	6 (0.3)^{e}
	ZP2	5 (0.2)	5 (0.3)	4 (0.2)
Bite size				
Cattle	ZP1	0.33 (0.02)^{f,g}	0.38 (0.01)	0.41 (0.01)^{f}
	ZP2	0.41 (0.04)^{g}	0.43 (0.03)	0.44 (0.04)
Donkey	ZP1	0.29 (0.01)	0.26 (0.01)	0.30 (0.01)
	ZP2	0.24 (0.17)	0.24 (0.02)	0.29 (0.02)
Bite size per $M^{0.75}$				
Cattle	ZP1	5.6 (0.38)	6.5 (0.11)^{h}	7.1 (0.32)^{h}
	ZP2	6.5 (0.62)	6.0 (0.10)	7.0 (0.51)
Donkey	ZP1	5.5 (0.43)^{k}	5.8 (0.43)	6.5 (0.67)
	ZP2	4.9 (0.35)^{j,k}	5.2 (0.47)	6.4 (0.33)^{j}
Rate of intake				
Cattle	ZP1	6.7 (0.5)^{l,m,o}	8.3 (0.18)^{q}	9.4 (0.27)^{l,r}
	ZP2	11.0 (0.74)^{m,p}	12.4 (0.96)^{q}	13.2 (0.92)^{m,r}
Donkey	ZP1	6.4 (0.64)^{s}	5.7 (0.08)	6.8 (0.28)
	ZP2	4.1 (0.21)^{o,s}	4.6 (0.39)	6.4 (0.32)^{o}

f,h,k Values that share the same superscript differ significantly ($P < 0.05$).

j,m,s Values that share the same superscript differ significantly ($P < 0.01$).

a,b,c,d,e,o,p,q,s Values that share the same superscript differ significantly ($P < 0.001$).

Access to grazing had a significant effect on bites-per-step in cattle (Table 8.13) during ZP1, when the animals with 8-hour access took significantly more bites-per-step than during the other 2 treatments ($P<0.001$). Cattle took significantly ($P<0.001$) more bites-per-step during ZP1 than during ZP2. The effect of species on bites-per-

step was season dependent, with cattle taking significantly ($P<0.001$) more bites-per-step than donkeys did during ZP1, but significantly ($P<0.001$) less during ZP2.

There was no significant effect of season on bite size by either species. Bite size was significantly larger ($P<0.001$) in cattle than in donkeys (Table 8.13). There were no significant treatment effects on bite size and the only seasonal effect occurred in the cattle given 24-hour access to grazing; bite size in ZP1 was significantly ($P<0.05$) less than during ZP2.

Comparison of bite size per unit of metabolic live weight (mg per $M^{0.75}$) between donkeys and cattle showed no significant difference between the 2 species. Other differences in bite size between treatment and season that became significant when data were expressed relative to metabolic weight need to be regarded with caution because of the weak relationship between live weight and bite size.

There were highly significant ($P<0.001$) differences between rates of intake by cattle and donkeys. Significant seasonal differences were apparent in both cattle ($P<0.001$) and donkeys ($P<0.01$). During ZP1, the only significant ($P<0.01$) treatment effect on rate of intake occurred between cattle with 24-hour access and those with 8 (Table 8.13). During ZP2, a similar effect of the treatments on rate of intake was seen in cattle as in ZP1 (Table 8.13). However, during ZP2, donkeys with 24-hour access to grazing had a significantly slower rate of intake than either donkeys with 11- ($P<0.01$) or 8-hour access ($P<0.001$).

8.4: Discussion

8.4.1: External marker recovery

The recovery rates of C_{36} alkane for both donkeys and cattle (93.2 and 91.3% respectively) were close to the value measured with sheep by Mayes, Lamb and

Colgrove (1986) and Dove *et al* (1989) (93.1 and 94.8% respectively). Alkanes are broken down to a small degree during their passage through the digestive tract (Dove and Mayes, 1991) and their degradability decreases as the number of carbon atoms in the alkane increases; the incomplete recovery of C_{36} in the present experiment may have resulted from partial digestion of the marker.

Recovery rates of Cr_2O_3 were in excess of 100% in both cattle and donkeys, perhaps due to circadian variation in marker output, not overcome by dosing twice per day.

Although C_{36} alkane was principally used as one part of an alkane pair to estimate DMI, it can also be used by itself to estimate FO, providing faecal concentrations are corrected for incomplete recovery. It would appear from this experiment that C_{36} is a better external marker because its recovery rate was more readily predicted than that of Cr_2O_3.

8.4.2: Reliability of dry matter intake estimations

In view of the lack of a 'gold standard' method for estimating DMI at grazing, the use of 3 methods to estimate DMI improved the confidence in the results, as overall there was no significant difference between the 3 methods. However, in some cases (Figure 8.7) estimates of DMI by the ALK method did provide results that were significantly different from the other 2 methods. Estimates of DMI obtained with the EM-IV and DMAmethods were similar, and gave values close to those predicted from live weight changes using the MAFF (1987) energy requirement system for cattle and INRA (Martin-Rosset *et al.*, 1994) energy requirement systems for equids. The use of C_{35} and C_{36} alkane pairs as markers was, in retrospect, a poor choice because of the small amount of C_{35} (mean concentration=20 mg/kg DM) in plant

samples. A better choice of alkane pair would have been C_{31} and C_{32} or C_{32} and C_{33}. The concentration of C_{31} and C_{33} in the diet sample was about 6 times higher than the concentration of C_{35}. Errors in the estimation of the more abundant alkanes of say ±5 mg/kg DM would have had a much smaller effect on the final estimate of DMI than if the same error was made with C_{35}.

8.4.3: Cattle

Effect of diet quality and time of access on dry matter intake

Cattle DMI during ZP2 was significantly ($P<0.001$) higher than that during ZP1. This difference in DMI was related to diet quality as there was little difference in feed availability and the prediction of VFI using the ARC (1980) model agreed with the values obtained during both experimental periods.

During ZP1, access time to grazing had no effect on DMI or LWG, despite the fact that animals with more time available to eat, spent longer grazing. Predicted VFI using the ARC (1980) model was 66.7 g DM per $M^{0.75}$, which was similar to the mean estimated DMI for cattle at 70.3 g DM per $M^{0.75}$.

Voluntary food intake (VFI) in Cattle may have been constrained during ZP1 by either sward structure or diet quality. If sward structure was limiting DMI, bite size would be expected not to exceed 0.3 g OM per bite which, Stobbs (1973) showed to be limiting in cattle grazing sparse tropical swards. The bite size of the animals with 8-hour access to grazing (0.38g OM per bite) could be considered to be the closest estimate of maximum bite size under the prevailing sward conditions, because these animals were under more pressure to achieve a VFI consistent with need. The estimate of maximum bite size during ZP1 was in excess of that found to be limiting to DMI by Stobbs (1973). Furthermore, the estimated total number of bites per day

by cattle during ZP1 never exceeded 13,000 per day, far below the 36,000 per day that Stobbs (1973) showed to be limiting. This suggests that DMI during ZP1 was not limited by sward structure but rather by diet quality.

During ZP2 the cattle with only 8-hour access ate significantly ($P<0.01$) less than the cattle in the other 2 groups, but still achieved a live-weight gain of 27 kg over a 3-week period. There was no significant difference between the DMI of cattle with 11- rather than 24-hour access, despite the fact that animals with free access to sward spent significantly longer grazing (Table 8.10). Sward conditions did not appear to limit DMI, as estimated DMI for the 11- and 24-hour groups exceeded those predicted by the ARC (1980) model.

Dry matter intake appeared to be limited by diet quality, with particularly low levels of CP, during ZP1, and providing cattle with more time to eat did not increase DMI because maximal VFI was achieved after 8-11 hours' grazing. During ZP2, DMI was constrained by the time available for eating and not by sward quality; cattle could not achieve maximal VFI when given only 8 hours in which to graze.

Comparison of feeding behaviour between ZP1 and ZP2

All cattle spent more time grazing during ZP2 than during ZP1, indicating that the lower quality of the sward during ZP1 was restricting VFI. With the exception of the 8-hour group, average ETPH was greater during ZP1 than during ZP2 with time spent eating per hour only falling below 50 minutes per hour in the final 2 hours of common grazing time (14:00-16:00h). In all treatment groups, feeding intensity during ZP2 was highest during the first 3 hours after release from the kraal (or in the case of the 24-hour access group, the first 3 hours after daybreak).

Bite rate was significantly lower during ZP1 than ZP2. As bite size changed little between the 2 periods, the difference in bite rate indicates that the number of required chews per bite was lower during ZP2. Presumably this was because the quality of the diet was better. Bites per step during ZP2 were much higher than in ZP1, indicating that animals were having to walk less between selected feeding stations. Overall, cattle during ZP2 were able to maintain a higher rate of intake than during ZP1 because both quality and abundance of forage facilitated a rapid bite rate.

Compensation for restricted access to grazing

During ZP1, there was little opportunity for cattle with 8-hour access to grazing to increase ETPH because most of the available time was already spent feeding. During the 1 hour of the day (12:00–13:00 h) when an opportunity did exist for increased ETPH, cattle with 8-hour access spent more time grazing than the other 2 treatment groups.

Both the 8- and 11-hour groups compensated for restricted feeding time by increasing bite rate. In the case of the 11-hour group, this strategy entirely compensated for restricted eating time and the DMI of this group was statistically no different from the free-access group. However, the 8-hour group could not increase bite rate sufficiently to compensate for restricted access to grazing; further increases in bite rate were presumably restricted by the number of chews required per bite.

Bite size during ZP1 also differed between treatments; cattle with 8-hour access to grazing took larger bites than the 24-hour group (Table 8.13). This increase in bite size was achieved at the expense of diet quality. The QI of the 8-hour group was significantly lower than for the cattle with free access to grazing (Table 8.9). Bites per step in the 8-hour group were higher than for both the other groups, indicating that

animals with the least amount of time to eat were spending more time at each feeding station and, therefore, probably being less selective in the food they ate (Ruyle and Dwyer, 1985). The bite size, bites per step and QI of the 11-hour group were intermediate to those of the 24- and 8-hour groups (Table 8.9 and 8.5).

During ZP2 cattle with 24-hour and 11-hour access had lower ETPH than the 8-hour group during the common grazing hours (08:00-16:00h). The 11-hour group increased bite rate but not ETPH presumably because accelerated bite rate was sufficient to compensate for reduced grazing access time. Bite rate of the 8-hour group was considerably higher than that of the 24-hour group but only marginally higher than that of the 11-hour group, suggesting that maximal bite rate had been reached.

Results from ZP1 and ZP2 suggest that cattle compensate for restricted grazing access by increasing bite rate and when possible, increasing ETPH. The primary response of cattle when confronted with restricted access time to feed, is to increase bite rate in an attempt to increase rate of intake. It appears from the present study that, on a given sward, cattle have a limited capacity to increase bite rate and any increase is achieved at the expense of diet quality. The secondary response of cattle to restricted grazing access is to increase ETPH. This 2-stage compensation strategy may be motivated by the cattle's desire to minimise time spent grazing per day, which can be explained in evolutionary terms as an attempt to reduce exposure to predators during grazing (Janis 1976). This instinct is likely to be stronger in African indigenous breeds that have been selected for survival characteristics (naturally or otherwise) than it is in European breeds that have been deliberately selected for production characteristics, an underlying trait of which is a greater drive to eat.

8.4.4: Donkeys

Effect of diet quality and time of access on dry matter intake

There were no significant differences in DMI between ZP1 and ZP2 in donkeys (Table 8.8) despite significant differences ($P<0.001$) in QI of the diet. This finding supports the theory of Pearson *et al.* (1998) that donkeys maintain high levels of DMI of poor quality feeds by decreasing MRT.

During both ZP1 and ZP2 increasing time of access to grazing from 11 to 24 hours had a significant effect on DMI. Donkeys with 11-hour access to food ate more than the donkeys with 8-hour access, but not significantly so.

Comparison of feeding behaviour between ZP1 and ZP2

Donkeys with free access to rangeland spent significantly more time grazing during ZP2 than ZP1. Grazing time in the other 2 groups increased between ZP1 and ZP2 to a small extent, but as 95% of the grazing access time was already used for feeding during ZP1, there was little opportunity for it to be increased during ZP2.

Bite rate was higher in donkeys during ZP1 compared to ZP2. The increased frequency of bites in donkeys during ZP1 is difficult to explain as there was no difference in bite size between the 2 seasons and diet quality was higher during ZP2. One possible explanation is that the donkeys took fewer chews per bite during ZP1, which would have resulted in increased faecal particle size. As neither chew rate nor faecal particle size were measured, this explanation is speculative in nature. There was no effect of season on step rate or bites per step.

There was a significant seasonal effect on intake rate by donkeys; on average they consumed forage at a slower rate during ZP2, reflecting a slower bite rate rather than a smaller bite size.

Compensation for restricted access to grazing

The ETPH during the common grazing hours in the 3 treatment groups were virtually identical to one another during both treatment periods. Time spent grazing per hour never fell below 55 minutes between 08:00 h and 16:00 h during ZP1. During ZP2, ETPH was less in all treatment in the hour between 13:00h and 14:00h, when animals typically went to drink and spent some time idling; donkeys with the least access to grazing spent more time grazing during this hour.

Bite rate of donkeys with 8-hour access to grazing was higher than in the other 2 treatments during both ZP1 and ZP2. There was little difference in bite rate between the 24- and 11-hour groups. However, increased bite rates allowed the animals with 8-hour access to achieve levels of DMI similar to that of the 11-hour group. The reason for the 11-hour group not responding to restricted grazing access by increasing bite rate is not clear, especially as this treatment group sustained similar live weight losses as the animals with 8-hour access during ZP1. One possible explanation was that as increased bites are achieved at the expense of diet quality (Table 8.9); the benefit of increased DMI may have been outweighed, in the case of the 11-hour group, by a decrease in diet quality.

The opportunities to compensate for restricted grazing access by donkeys are limited to increasing bite rates. This process results in a reduction in diet quality and donkeys appear reluctant to 'sacrifice' diet quality for DMI.

8.4.5: Comparison of the foraging strategies of cattle and donkeys

Results from this experiment have shown that donkeys and cattle have radically different foraging strategies that affect the response of the 2 species to both season and access time to rangeland.

Dry matter intake

The response of donkeys and cattle to season in terms of DMI were opposite. During the dry season (ZP1), when diet quality was low, the DMI per kg $M^{0.75}$ of cattle was lower than that of donkeys, whilst during the wet season (ZP2), when diet quality was high, cattle ate more than donkeys.

The results from ZP1 indicate that donkeys have a higher VFI relative to body mass than cattle. This finding agrees with the hypothesis of Janis (1976), which states that the digestive strategy of equines is one of high input and throughput with relatively low extraction efficiency. The same hypothesis suggests that equids are less selective feeders than cattle. This is not supported by the findings from the current experiment because donkeys consistently selected a diet of better quality than that selected by cattle.

The foraging strategy of cattle and donkeys when grazing quality is high (ZP2) is difficult to determine from this experiment because the effects are compounded by differences in the maturity of the 2 species.

Feeding behaviour

Feeding behaviour of donkeys and cattle were dissimilar in many respects. Time spent feeding was significantly greater in donkeys than in cattle with the same access time to grazing in all but the 8-hour groups during ZP2 (Table 8.10). When given the opportunity donkeys would use the hours of darkness to graze, whilst cattle stopped grazing almost immediately when the sun went down. ETPH of donkeys during daylight hours was higher (57 minutes per hour) than in cattle (46 minutes per hour). Cattle had greater bite rates during ZP2 than during ZP1, whilst bite rate was higher in donkeys during ZP1. Less rapid bite rates in cattle during ZP1 can be explained by

the lower quality of the diet, which took longer to comminute than during ZP2, so retarding bite rate. The reason for the higher bite rate in donkeys during ZP1 is not clear and more detailed investigation must be conducted.

Bites per step can be used as an indicator of the type of selection practised by the animals. Overall, donkeys were more selective, achieving a diet quality that was 2.3 times higher than mean sward quality, compared to cattle, which achieved a diet quality 1.7 times higher than mean sward quality. Bites per step in cattle were related to the QI of the diets, whilst in donkeys there was no effect of QI on bites per step (Figure 8.18). This indicates that although donkeys achieved a diet quality higher than that of cattle, it was not achieved by decreasing time spent per feeding station but rather by selecting within the sward canopy.

8.5: Conclusions

Restricting time of access to grazing has a greater effect on the DMI of donkeys than of cattle; this is because donkeys with free access to grazing spend longer grazing (16 hours per day) than cattle (10 hours).

Cattle with 11-hour grazing access achieved a DMI similar to those of cattle with 24-hours access. The DMI of cattle with 8-hour access to grazing was only affected by the restricted grazing time during ZP2, when DMI was not limited by diet quality.

In cattle, compensation for restricted time of access to grazing was made, firstly, by increasing bite rate, then by increasing ETPH. Increased bite rate was achieved at the expense of diet quality in cattle with 8-hour access to grazing during the dry season (ZP1).

In donkeys, increasing the time available for eating from 8 to 11 hours had no significant effect on DMI; these 2 groups spent 95%of the available access time

grazing. Donkeys with 24-hour access had higher DMI than the other 2 treatment groups and ETPH of this group was similar to that of the other 2 groups during the common grazing hours. There was no opportunity for donkeys to compensate for restricted grazing time by increased ETPH. Donkeys appeared reluctant to increase bite rate to compensate for restricted eating time. Only during the dry season (ZP1) did donkeys with 8-hour access to grazing increase bite rate to a significant degree and this was achieved at the expense of diet quality. Maintaining diet quality by selection appears to be the main priority of donkeys.

CHAPTER 9

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

9.1: Introduction

Restricted nutrient intake is the largest single factor that limits the productivity of grazing animals (Hodgson, 1982b). Traditional African grazing systems (TAGS) appear to exacerbate this constraint by restricting the amount of time available to feed. This project set out to investigate the effect of TAGS on the forage intake by free ranging cattle and donkeys in order that recommendations for their improved nutrition and productivity could be formulated and disseminated to resource-poor livestock owners of Africa. This investigation presented 2 major challenges; the first was to develop and test techniques that could be reliably applied under tropical rangeland conditions (method development); the second was to carry out detailed studies on herbivore foraging behaviour under TAGS (range-land access) and as a consequence this thesis is presented in 2 sections. The practical implications for the management of cattle and donkeys are discussed below, together with the priorities for further research.

9.2: Method development

9.2.1: Estimation of dry matter intake at grazing using the ratio technique

The problems associated with the measurement of DMI by free-ranging animals and the currently available techniques were discussed in Chapter 2. Although imperfect, the ratio technique was considered most suitable for application under rangeland conditions. Several research objectives were established with the aim of improving the reliability of the ratio technique under these conditions. These objectives were: 1) to develop techniques for the rapid and efficient dosing of external markers to

both donkeys and cattle; 2) to test the suitability of various internal markers for the estimation of DMD in both donkeys and cattle; 3) to develop *in vitro* techniques for the estimation of DMD that could be applied to donkeys; 4) to develop sampling procedures that would provide representative samples of ingesta on a quantitative basis; 5) to test the suitability of the alkane-pair method of estimating DMI under tropical rangeland conditions; 6) to improve confidence in DMI estimates using several simultaneous techniques. The work presented in this thesis describes the development and testing of several methods that succeeded in addressing the above objectives and resulted in improvement in the reliability of the ratio technique under rangeland conditions.

A rapid method for simultaneously dosing even-chain alkane and Cr_2O_3 markers that could be readily applied to both equids and cattle was developed (Chapter 3.1). This system involved twice daily dosing, which resulted in a more even distribution of marker throughout the gut, thereby reducing circadian variation in faecal marker concentrations.

Several internal markers, used to estimate DMD *in vivo*, were tested; ADL was the most reliable (Chapter 3.2). However, the recovery rates of this marker must be established using penned animals, in order that the measured values of ADL in the faeces could be adjusted for incomplete recovery.

An *in vitro* DMD technique, based on Tilley and Terry (1963), was developed that provided more reliable estimates of *in vivo* DMD than the unmodified TT techniques when used in equine species (Chapter 3.3). The modified method was used successfully to estimate the DMD of forage consumed by donkeys in Zimbabwe (Chapter 8).

Obtaining a representative sample of ingesta remains a major problem if ratio methods are to be used to estimate DMI at grazing. Extrusa collected from oesophageal-fistulated animals remains the method of choice for most pasture research scientists. The reliability of this method for collecting ingesta samples from free-ranging herbivores is questionable. Increasing sampling frequency of oesophageal extrusa has been made possible by use of the RCOFV, however, this technique can only be applied to small ruminants at present, and it is unlikely that it could ever be used with equid species. In the Zimbabwe study (Chapter 8), the method of obtaining representative dietary samples was by rigorous hand-plucking.

The selection of C_{35} and C_{36} alkanes to estimate DMI at grazing (Chapter 8), proved to be a poor choice because of the low concentrations of C_{35} in tropical grasses which resulted in an unacceptable level of error (C.V. 54%). The levels of C_{29}, C_{31} and C_{33} were typically 10 x greater than that of C_{35}, and would have provided more reliable estimates of DMI. The use of an even-chain alkane (C_{36}) to estimate faecal output proved more reliable than Cr_2O_3 because recovery rates of the alkane were predictable and correction factors obtained from penned animal trials could be applied with confidence.

During the Zimbabwe study (Chapter 8), several methods of estimating DMI were attempted simultaneously. Two external markers were fed (C_{36} and Cr_2O_3) and the double marker (ADL and C_{36}), alkane pair (C_{35}/C_{36}) and external marker (C_{36}) / *in vitro* DMD techniques were used to estimate DMI at grazing. When recovery values for external and internal markers, obtained from parallel-penned trials were applied, there was no significant difference between DMI estimates obtained using the 3 techniques (although the alkane pair method showed the greatest amount of variation

[C.V. 54%] for the reason described above). The close agreement between the 3 techniques increases confidence in the accuracy of the estimated values because each technique had different sources of error. Whilst this does not necessarily indicate that estimated DMI was close to the quantity of dry matter consumed, a theoretical comparison between estimated DMI and predicted DMI using energetic models also showed close agreement. The use of simultaneous techniques required no extra fieldwork, although laboratory analysis was increased, and thus, these techniques can be applied as readily as a single method under rangeland conditions.

The techniques used to estimate DMI at grazing are still imperfect, but this project has contributed to both the testing and development of novel measurements of nutrient intake in free-range animals. More work is still required for the development of appropriate techniques, particularly in respect to the collection of quantitatively representative samples of consumed forage. The unreliability of current methods of collecting consumed forage represents the single, greatest limiting factor to the reliability of measurements of DMI by animals at grazing.

9.2.2: Automation of behavioural data collection and processing

The foraging behaviour of herbivores on rangeland is a valuable indicator of the response of animals to both the abundance and quality of the available food resource. The comparisons between different species and grazing access treatment groups in terms of feed related time budgets, circadian, prehension and comminution activity were central techniques used to explore BCS in animals with RFT.

Both the collection and processing of behavioural data are laborious and error-prone tasks. The partial or complete automation of behavioural data collection reduces both the labour demands and errors associated with traditional manual methods of

behavioural recording. Three methods of automation of behavioural data collection are described in this thesis. The objective of this research was to develop and test automated methods of behavioural data collection with a view to reducing labour demands together with improving the accuracy of behavioural studies.

Firstly, a Psion datalogger was programmed to prompt observers to enter behavioural data, which were then stored on an internal memory chip (Chapter 4.2). After downloading onto a personal computer, the digital data could be processed with standard word-processing and spreadsheet software. This system automated both the recording and processing of behavioural observational data, but still required a trained observer to enter the information. The system was designed to provide maximum flexibility to the person making the data entries, so that any unusual or additional behaviour could also be recorded. This system was used extensively in both Ethiopia and Zimbabwe to collect behavioural data. Apart from some minor problems with power supply management, the system proved more reliable and less laborious than traditional paper techniques.

Two other systems were developed and tested for the automation of behavioural data collection. A telemetric system, using a resistive transducer, was built especially for the current project (Chapter 4.3). This system was tested in the UK and Ethiopia. After several months of development the system was abandoned because its use proved too laborious and the data it provided could not readily be correlated with actual feeding behaviour. The second fully automated system, the IPRED was found to be a useful aid to the collection of behavioural data following minor modification (Chapter 4.4); this system was successfully tested in Zimbabwe (Chapter 8). With practice, this system could be used to gather supplementary data in addition to that

collected by manual means and could also be used when manual methods were unworkable, such as during the hours of darkness. It was found to be particularly useful for equids when it was unnecessary to distinguish between eating and rumination behaviour. It was concluded that whilst devices for the complete automation of behavioural data collection were useful, they could not totally replace manual observations.

Two systems developed and tested during this project were used to collect most of the behavioural data presented in this thesis. The automation of behavioural data collection simplified and reduced the labour demand during field observations, freeing manpower to make more detailed, focal observations, including activities such as step and bite counts. In addition, the IPRED devices allowed night-time observations to be made.

9.3: The effect of restricted grazing time on dry matter intake and foraging behaviour

The penned-animal trial and rangeland studies described in earlier chapters (6, 7 and 8) demonstrated the effect of TAGS on DMI in 2 important, domesticated herbivore species, cattle and donkeys. The objectives of this research were: 1) to investigate the interacting effects of restricted feeding time, diet quality and forage availability on the dry matter intake of cattle and donkeys; 2) compare the foraging strategies of cattle and donkeys; 3) to examine any behavioural compensation strategies of cattle and donkeys managed under TAGS; 4) investigate the management implications of TAGS and explore sustainable alternatives for improving animal productivity.

9.3.1: The effect of diet quality and forage availability on dry matter intake

The penned-animal trial (Chapter 6) showed that time spent eating was related to food quality and ease of eating and that donkeys, ponies and cattle all strive to maximise rate of intake. However, under rangeland conditions, the effect of diet quality on time spent eating was confounded by forage availability. During the dry season (ZP1) cattle in Zimbabwe took smaller bites and more steps per day than during the wet season (ZP2), as a consequence they expended more effort to achieve a lower DMI. Donkeys had similar DMI during both the dry (ZP1) and wet seasons (ZP2) but they took more steps per day and had smaller bite sizes during the wet season (ZP2) than during the dry. Consequently, less effort was expended foraging when forage quality was low (ZP1) than when it was moderate (ZP2). Cattle in Ethiopia spent similar amounts of time grazing during both the wet and dry seasons, and achieved similar levels of DMI; dry herbage mass during the wet season was almost 5x greater (131 g/m^2) than during the dry season (37 g/m^2). The influence of forage availability and quality on DMI has not been fully resolved by the work reported in this thesis. Further research is required to investigate the effect of forage availability, forage quality and sward structure on the DMI of cattle and donkeys grazing tropical rangelands during all seasons, especially in the communal areas.

9.3.2: The effect of restricted feeding time on dry matter intake and foraging behaviour

In both Ethiopia and Zimbabwe, RFT had no significant effect on the DMI of cattle except, in Zimbabwe the 8-h grazing group, during the wet season (ZP2) when DMI was reduced. The groups with reduced access increased the amount of time spent per hour grazing (where possible) and increased bite rate to compensate for RFT. Donkeys in Zimbabwe ate less as the time available for eating was decreased from

23 to 11-h. This effect was more pronounced during the wet season (ZP2) than during the dry (ZP1).

The penned-animal trial showed a clear inverse relationship between bite size and bite rate; as bite size increased the rate fell. This relationship has important ramification on possible BCS for RFT, because bite rate was constrained by bite size and, therefore, an animal's ability to increase bite rate to compensate for RFT was strictly limited. When herbivores are foraging upon rangeland, intervals between bites are likely to be prolonged by selection and search activities. In this situation, increasing bite rate to compensate for RFT was less constrained by bite size than it is in pen-fed animals.

The rangeland studies highlighted several behavioural compensation strategies that cattle adopted to compensate for loss of eating time. They were to increase bite rate, increase ETPH and increase the number of bites per step. Compensation strategies by donkeys have not been clearly identified and further studies are required to investigate the response of these animals to restricted grazing time under different sward conditions. The following discusses the foraging strategy of the species studied and goes on to explore the implications for grazing management.

9.4: Foraging strategies

The foraging strategies of the indigenous breeds of African cattle can be considered to be close to those of the wild bovids of the continent. In evolutionary terms, the slow moving, wild bovids were thought to have developed rumination as an anti-predation strategy, with exposure-time to danger being minimised during grazing by postponement of comminution (Kingdon, 1997; Janis 1976). As the hunting activity of the major predators (lion, leopard and hyena) of large African bovids is largely

confined to nocturnal periods (Haltenorth and Diller, 1988), the avoidance of grazing during the hours of darkness may be a part of this anti-predation strategy.

Whilst anti-predation strategies may have explained the rare occurrence of night grazing by Zimbabwean cattle during this study, the total absence may have been caused by allelomimetic behaviour of the group with free access to grazing (Alhassan and Kabuga, 1988) associating with the other animals in the herd which were kraaled during the night. However, other workers (Harker, Taylor and Rollinson, 1956; Lampkin and Quarterman, 1958) have recorded little night-grazing by indigenous breeds of African cattle under free ranging conditions; night-grazing activity seldom represented more than 5% of the total time available for grazing. Smith (1959) and Wilson (1961) reported that night-grazing by African zebu breeds kept in paddocks could occupy up to 4 hours of the night-time activity, particularly during the dry season when forage was in short supply. However, this was atypical and 2 hours per night was more normal. Smith (1961) also reported a mean grazing times of 2.2 hours between 18:00h and 07:00h by indigenous breeds of African cattle under free-range conditions, although not all of this observation period would have been during the hours of darkness.

Night grazing by exotic breeds of cattle in the tropics has been reported to make a greater contribution to the total grazing time than for indigenous breeds. Mugerwa, Christensen and Ochetim (1973) reported that night-grazing represented 30–46% of the total grazing time of lactating Friesian cows in Uganda. Similar values (32%) where reported by Goldson (1963) for lactating Jersey cows in Kenya. Alhassan and Kabuga (1988) made a direct comparison between exotic and indigenous breeds in

Ghana, reporting that Friesian bulls spent more time grazing at night than indigenous N'dama bulls that grazed the same paddock.

The differences in night time grazing behaviour between indigenous and exotic breeds of cattle may have resulted from deliberate selection of exotic breeding animals for performance characteristics such as growth rate and milk yield. This breeding process may have brought about an incidental increase in the drive to eat in each progressive generation, resulting in the need to utilise the hours of darkness to complete the feeding motivation. Natural selection by the indigenous breeds is likely to have favoured animals that avoided grazing during the hours of darkness because they would have been more likely to survive predation.

Anti-predation strategies were manifested by attempts to minimise the amount of time spent grazing and to maximise the rate of intake. This may explain the hierarchy of behavioural compensation by cattle in both Ethiopia and Zimbabwe, who responded to a reduction in time-of-access to grazing, firstly, by increasing bite rate and then, by increasing ETPH.

The wild ass (Equus africanus), the ancestor of the domesticated donkey (Equus asinus), evolved in the semi-desert grasslands of Northeast Africa, preferring rocky hills to sandy areas (Kingdon, 1997). Its foraging strategy was distinct from that of the other equids described by Janis (1976), although it is still predominantly a grazer rather than a browser (Haltenorth and Diller, 1988). The wild ass is mostly a nocturnal grazer, spending most of the daylight hours resting (Haltenorth and Diller, 1988).

From the limited number of studies that have been conducted, the feeding preferences of the domesticated donkey appear similar to those of its wild ancestor; browse being of secondary importance to grass in the diet (Pearson and Nengomasha 1994; Rudman, 1990; Moehlman *et al.,* 1998).

In some respects, the foraging strategy of donkeys conforms to the generalised equid strategy postulated by Janis (1976). The research reported in this thesis established that DMI relative to bodyweight was maintained at around 2% regardless of the quality of the sward, indicating that MRT was similar during both the wet and dry seasons. Reduced retention times of poor quality forages would be expected to result in a depression of DMD. Examination of the donkey data from the Zimbabwe research indicated that this was, indeed, the case. Low quality diets gathered during the dry season had substantially higher (32%) potential DMD, estimated by *in vitro* techniques compared to *in vivo* DMD, estimated with ADL marker.

However, the digestive strategy of donkeys appears to be better able to cope with the subtleties of forage availability than Janis's (1976) theory would suggest. The Zimbabwean data indicated that the difference between potential DMD and *in vivo* DMD diminishes as DMI decreases (resulting in this case from restricted grazing access). Pearson *et al. (*1998) showed the same effect in donkeys fed restricted and *ad libitum* quantities of chopped alfalfa; MRT was higher when animals had a restricted ration. These authors failed to show the same effect when donkeys were fed oat straw, although in this case, the difference between the DMI per unit of metabolic live weight during ad libitum and restricted treatments was only 7 g/kg $M^{0.75}$. Furthermore, MRT of the alfalfa and oat straw diets in donkeys during the restricted treatments were very similar to one another (40 and 38 hours respectively).

From these results it would appear that in donkeys, MRT and, therefore, DMD, are more dependent on level of intake compared to ruminants, where level of intake is more dependent on MRT (Forbes, 1986). This ability of the donkey to adapt MRT to the level of forage intake provides an invaluable adaptation to arid rangeland conditions. When forage is plentiful, but of poor quality, MRT and DMD are low with nutrient intake being maintained by high levels of DMI. When available forage is sparse, DMI decreases, resulting in higher MRT and a more efficient digestion, thereby maintaining levels of nutrient uptake.

The foraging strategy of donkeys also departs from that of the generalised equid strategy proposed by Janis (1976) in terms of the type of material selected from swards. Janis (1976) suggested that equidae tend to select stalk rather than leaf (i.e. select for fibre), based on the observations of Burchell's zebra (*Equus burchelli*) and wildebeest (*Connochates taurinus*) by Bell (1969); the equid selected more stem material than the ruminant. The results from the Zimbabwean study show that donkeys do not conform to the strategy proposed by Janis (1976). The penned-animal trial also showed that donkeys and ponies are more selective than cattle; the equids selected against the bitter tasting leaves of alfalfa to a greater degree than cattle.

Donkeys spent a greater proportion of their day grazing than cattle. In particular, the hours of darkness were utilised extensively for grazing; a maximum of 17 h grazing per 24 h were recorded in the wet season during the Zimbabwean study. The increased grazing time resulted in a greater nutrient intake in terms of both quantity and quality of food eaten.

The findings from the present study show that donkeys are highly selective foragers and that this selection occurs within the plant canopy, rather than by horizon or patch selection. Donkeys obtain higher quality diets than cattle when grazing the same forage resource. Furthermore, the DMI of donkeys was not constrained by sward quality as it was in cattle and MRT was closely related to level of intake.

9.5: Management implications

The tendency of indigenous breeds of African cattle to avoid night grazing, or at least to reduce it to an absolute minimum, has important implications for grazing management. Extension of grazing time beyond the hours of daylight has little effect on the DMI of cattle, especially if the cattle are able to attain maintenance levels of DMI during daylight hours. Additional access to grazing during the night may be beneficial if forage is sparse and if cattle are seriously undernourished. Conversely, additional access may also be of value for short periods during the wet season when time available for feeding is the major constraint to DMI, rather than sward quality or availability.

Providing grazing for cattle at night (whether exotic or indigenous breeds) may be beneficial for animals that have been systematically selected for production traits because these are more likely to utilise these hours of darkness to graze. The provision of night grazing may also be beneficial during seasons of the year when hot or humid conditions reduce grazing during daylight hours (as a result of animals seeking shade). Further research is required to quantify the impact of breed and environment on the DMI of cattle with RFT.

Providing cattle with the maximum amount of daylight grazing (12 h) had beneficial effects on cattle DMI in the Zimbabwean study but had no significant effect during

the Ethiopian study. Ethiopian cattle with 8-hour access to grazing achieved similar levels of DMI to their conspecifics with 11-hours access but still had relatively low mean daily ETPH of 46 minutes per hour; mean ETPH in Zimbabwe was 52 minutes per hour. Studies by Smith (1961) of cattle with 7-hour access to Hyparrhenia rangeland in Zambia recorded similar mean daily grazing intensities (51 minutes per hour) to those measured in the Zimbabwean study reported herein. Haggar (1968) reported low grazing intensities (33 minutes per hour) by hay- and silage-supplemented Fulani bulls with 11-hour access to rangeland. This finding concurs with that of the Ethiopian study which showed grazing activity to be related to the satiety status of the cattle.

Hay supplementation of cattle during kraaling resulted in less forage being grazed and had no economic benefit, in the Ethiopian study. In terms of utilisation of a communal forage resource, provision of hay supplementation would not be successful for individual farmers because cattle eat less of the common, more readily utilised, forage resource. In certain situations, hay supplementation may be beneficial but only when forage availability or time of access limits the DMI of cattle at grazing. Where cattle are achieving a satisfactory DMI from grazing, hay supplementation will have no economic benefit to farmers who rely principally on communal grazing to feed their cattle.

Traditional African grazing systems have little effect on the DMI of cattle providing, that at least 8-hours of grazing access are provided per day, however cattle are better able to satisfy their DM requirement if provided with 12-hours feeding time. The exact amount of time required for cattle to achieve maximal DMI depends on the availability and quality of forage and the structure of the sward. In dense, closed

swards, such as those dominated by P. clandestinum, rapid intake rates are possible and maximal DMI is achieved in less time than on swards with an open tussock structure, such as those dominated by *Hypparrhenia* spp., *Seteria* spp. or *T. triandra.*

Cattle with RFT compensate for the loss of foraging time by increasing ETPH and bite rate. Both these strategies have limited capacity to compensate for RFT, therefore, where possible, cattle should be provided with the maximum amount of access to grazing during daylight hours (~ 12 h). Provision of 12-h of grazing access allowed cattle to exhibit their natural behavioural circadian rhythm and was thus unlikely to result in depression of DMI due to RFT.

The foraging strategy of donkeys is distinct from that of cattle; grazing management must reflect these differences. In particular, restricting time of access to grazing has a greater effect than it does on cattle; in donkeys restricting access to grazing to less than 12-hours resulted in a depression of DMI. This is particularly important when donkeys are used as working animals. Typical working times for donkeys in Zimbabwe are between 3 and 6-hours per day (Nengomasha, 1997) and frequently grazing is the only source of forage. Under TAGS, the nutrient intake of donkeys will be adversely affected by both a decrease in the amount of DM consumed and a reduction in the quality of the ingested forage. Allowing donkeys to night-graze would compensate for loss of eating time during daylight hours. However, unsupervised night-grazing of donkeys can cause damage to crops. Often this proves detrimental to both human and animal welfare; when caught, marauding donkeys are often brutally killed or injured by farmers (J. Redmond, Donkey Sanctuary, Bulawayo, Zimbabwe; personal communication).

Fenced night paddocks, or effective barriers around crops would allow donkeys to graze unsupervised at night, but the cost of fencing is prohibitive. Providing a limited amount of poor quality, supplementary fodder in the kraal at night would provide a sustainable method of compensating for the loss of feeding time. In cattle hay supplementation would generally depress the intake of the communal, pastoral feed resource. Donkeys that are closer to satiety select a better quality diet than when hungry, and would, therefore, make more efficient use of any communal feed resources. The amount of supplementary fodder offered to each animal should be limited, to ensure that they are still motivated to feed at grazing and that the majority of the dietary DM would still be obtained there.

Providing small amounts of concentrate feed (0.3–0.5 kg per animal) would probably have a more beneficial effect than supplementary fodder, as the effect of level of intake on MRT would be less pronounced; consequently, fodder consumed at grazing would be digested more efficiently. Whether this is a viable option for poor farmers in developing countries is questionable. By-products from small-scale on-farm crop processing and kitchen waste could possibly fulfil this role, although donkeys would have to compete with meat-producing livestock, such as goats, for this resource.

The nutritional cost/benefit of providing fodder or concentrate supplements to donkeys with restricted access to grazing is clearer than it is for cattle. Donkeys with less than 12-hour grazing time have lower DMI than those with free access to grazing, regardless of forage availability or quality. Donkeys are seldom used for anything other than to provide power and the benefit of sustained work may not outweigh the costs both in terms of effort and lost productivity by other classes of

livestock. Where and when possible, the most economic option would be to provide donkeys with night grazing.

9.6: Research Priorities

The research work presented in this thesis has identified the effects of TAGS on the DMI of both donkeys and cattle. However, the effects of TAGS under a range of different rangeland types and conditions have not been fully resolved and further research is required. Given unlimited funding, the following research investigations should be given priority:

Methodology

Testing the use of C_{31}/C_{32} or C_{33}/C_{32} alkane-pairs to measure intake using penned animals fed tropical grasses and browse in order to establish the reliability of the alkane method under range conditions.

Comparison of hand-plucking and oesophageal-fistula methods of ingesta sampling in order to establish the frequency required for attaining quantitatively representative samples.

Further verification trials of the modified *in vitro* DMD technique described in this thesis (Chapter 3) using a wider variety of foods, with a view to establishing reliable regression equations for the prediction of *in vivo* DMD in equids from values determined *in vitro*.

More rigorous testing of the IPRED bite meter under tropical conditions to reduce the incidence of data loss and to improve the differentiation of eating ruminating and pest related activities.

Rangeland Studies

Investigation of the effects of herbage structure, season, forage quality and rangeland species composition on DMI, particularly under drought conditions and where stocking rate is high.

The effect of TAGS on DMI and foraging behaviour under conditions of drought, high stocking rate, and other situations where forage availability is low.

The study of foraging behaviour of livestock on communally managed rangeland away from the contrived conditions of the research stations using the modified techniques described in this thesis.

Resolving the mechanisms by which donkeys select better quality forage than cattle when managed under the same rangeland conditions by examining the botanical composition of the diet using microhistological techniques.

9.4: Conclusions

The present study has attempted to address some of the issues surrounding the management of rangeland resources for cattle and donkeys of livestock owners in Africa. Restricting the grazing time of cattle to only 8-hours per day had no effect on DMI of cattle in both Ethiopia and Zimbabwe. Cattle compensate for RFT by increasing ETPH and by increasing bite rate. Traditional grazing management in African communal systems, therefore, does not appear to limit nutrient intake by cattle to a great extent. However, when forage was very sparse the effect of RFT was not examined, and further research is required to determine DMI under conditions of forage shortage.

The effect of TAGS on the nutrient intake by donkeys is much greater than in cattle; restricting the time available for eating limits DMI and reduces the quality of ingested forage. Donkeys must, therefore, be managed separately from cattle. This is particularly important when they are used for work. Donkeys are much less able to compensate for loss of eating time when working than are cattle, because they have evolved to spend much more time eating.

REFERENCE LIST

Aganga, A. A., Tsopito, C. M., & Seabo, D. (1994). Donkey power in rural transportation - Botswana case study. *Appropriate Technology,* 21: 32-33.

Agricultural Research Council (ARC). (1980). *The nutrient Requirements of ruminant livestock,* Technical Review by ARC Working Party. CAB, (pp 59 - 64) Farnham Royal, UK.

Alhassan, W. S., & Kabuga, J. D. (1988). Dry and wet season studies of the grazing behaviour of native N'dama cattle and imported Friesian bulls in a humid tropical environment. *Applied Animal Behaviour Science,* 19: 245-254.

Allden, W. G. (1962). Rate of herbage intake and grazing time in relation to herbage availability. *Proceedings of the Australian Society of Animal Production,* 4: 163 -166.

Arnold, G. W. (1984a). Comparison of the time budgets and circadian patterns of maintenance activities in sheep, cattle and horses grouped together. *Applied Animal Behaviour Science,* 13, 19-30.

Arnold, G. W. (1984b). Spatial relationships between sheep, cattle and horse groups grazing together. *Applied Animal Behaviour Science,* 13: 7-17.

Arnold, G. W., & Dudzinski, M. L. (1978). *The Ethology of Free-ranging Animals.* (pp 1 -15), Elsevier, Amsterdam.

Association of Official Analytical Chemists. (1990). *Official Methods of Analysis of the Association of Analytical Chemists* (15th ed.). (pp 10 -55) Association of Analytical Chemists, Virginia, USA.

Balch, C. C. (1958). Observations on the act of eating in cattle. *British Journal of Nutrition,* 12: 330-345.

Bayer, W., & Otchere, E. O. (1985). Effect of livestock-crop integration on grazing time of cattle in a sub-humid African savannah. In: J. C. Tothill & J. C. Mott (Eds.), *Ecology and Management of the World's Savannahs* (pp. 256-259). Australian Academy of Science, Canberra, Australia.

Bayer, W., & Waters-Bayer, A. (1991). Relations between cropping and livestock husbandry in traditional land use systems in tropical Africa. *Animal Research and Development,* 34: 57-69.

Bayer, W., & Waters-Bayer, A. (1998). *Forage Husbandry (The Tropical Agriculturalist).* (pp 1 -20) CTA / Macmillan, London.

Beauchemin, K. A., Zelin, S., Genner, D., & Buchanan-Smith, J. G. (1989). An automatic system for quantification of eating and ruminating activities of dairy cattle housed in stalls. *Journal of Dairy Science*, 72: 2746-2759.

Bell, R. H. V. (1969). The use of the herb layer by grazing ungulates in the Serengeti. In: A. Watson (Ed.), Animal Populations in Relation to Their Food Resources. *Symposium of the British Ecological Society* (pp. 111-128). Blackwell Scientific Publications, Oxford.

Blakeway, S. J. (1994). The welfare of donkeys. *M.Sc. Thesis*, University of Edinburgh (pp 20 - 30).

Block, E., Kilmer, L. H., & Muller, L. D. (1981). Acid insoluble ash as a marker of digestibility for sheep fed corn plants or hay and for lactating dairy cattle fed hay *ad libitum*. *Journal of Animal Science*, 52: 1164-1169.

Brandyberry, S. D., Cochran, R. C., Vanzant, E. S., & Harmon, D. L. (1991). Effectiveness of different methods of continuous marker administration for estimating faecal output. *Journal of Animal Science*, 69: 4611-4616.

Brouillette, J. P., Pell, A. N., & Welch, J. G. (1993). A portable electronic device that quantifies the eating and rumination activities in dairy cattle. *American Dairy Science Association and North East ADSA/ASAS Meeting, 88th Annual Meeting*, June 13-16, 1993, Abstract no. P405, pp 282.

Buntinx, S. E., Pond, K. R., Fisher, D. S., & Burns, J. C. (1992). Evaluation of the Captec chrome controlled-released device for the estimation of faecal output by grazing sheep. *Journal of Animal Science*, 70: 2243-2249.

Cameron, M. G., Fahey, G. C., Clarke, J. H., Merchen, N. R., & Berger, L. L. (1991). Effects of feeding alkaline hydrogen peroxide-treated wheat straw-based diets on intake, digestion, ruminal fermentation, and production responses by mid-lactation cows. *Journal of Animal Science*, 69: 1775-1787.

Canacoo, E. A., & Avornyo, F. K. (1998). Day time activities of donkeys at range in the coastal savannah of Ghana. *Applied Animal Behaviour* Science, 60: 229-234.

Canaway, R. J., Raymond, W. F., & Taylor, J. C. (1955). The automatic recording of animal behaviour in the field. *Electronic Engineering*, 27: 102-105.

Casson, T., Rowe, J. B., Thorn, C. W., & Harris, D. (1990). The use of natural n-alkanes in medic and clover as indigestible markers. *Proceedings of the Australian Society of Animal Production,* 18: 462.

Chambers, A. R. M., Hodgson, J., & Milne, J. A. (1981). The development and use of equipment for the automatic recording of ingestive behaviour in sheep and cattle. *Grass and Forage Science*, 36: 97 - 105.

Cheeke, P. R., Pedersen, M. W., & England, D. C. (1978). Responses of rats and swine to alfalfa saponins. *Canadian Journal of Animal Science*, 58: 783-789.

Coates, D. B., Schachenmann, P., & Jones, R. J. (1987). Reliability of extrusa samples collected from steers fistulated at the oesophagus to estimate the diet of resident animals in grazing experiments. *Australian Journal of Experimental Agriculture*, 27: 739-745.

Cochran, R. C., Adams, D. C., Wallace, J. D., & Galyean, M. L. (1986). Predicting digestibility of different diets with internal markers: evaluation of four potential markers. *Journal of Animal Science*, 63: 1476-1483.

Cochran, R. C., Vanzant, E. S., & DelCurto, T. (1988). Evaluation of internal markers isolated by alkaline hydrogen peroxide incubation and acid detergent lignin extraction. *Journal of Animal Science*, 66, 3245-3251.

Colbert, E. H. (1969). *The Evolution of the Vertebrates* (2nd ed.). (pp 535 -540)John Wiley and Sons, New York.

Cordova, F. J., Wallace, J. D., & Pieper, R. D. (1978). Forage intake by grazing livestock: A review. *Journal of Range Management*, 31: 430-438.

Cuddeford, D., & Hughes, D. (1990). A comparison between chromium-mordanted hay and acid-insoluble-ash to determine apparent digestibility of a chaffed, molassed hay/straw mixture. *Equine Veterinary Journal*, 22: 122-125.

Cuddeford, D., Pearson, R. A., Archibald, R. F., & Muirhead, R. H. (1995). Digestibility and gastro-instestinal transit time of diets containing different proportions of alfalfa and oat straw given to Thoroughbreds, Shetland ponies, Highland ponies and donkeys. *Animal Science*, 61, 407-417.

de Bruyn, T. D., & Marais, J. P. (1996). A preliminary investigation on the use of n-alkanes as a method of estimating digestibility and dry matter intake of goats (Poster Presentation). *Bulletin of the Grassland Society of Southern Africa,* 7(Suppl. 1): 84.

Demment, M. W., & Greenwood, G. B. (1987). The use of a portable computer for real-time recording of observations of grazing behaviour in the field. *Journal of Range Management*, 40, 284-285.

de Ridder, N., & Wagenaar, K. T. (1986). A comparison between the productivity of traditional livestock systems and ranching in eastern Botswana. In: P. J. Joss, P. W. Lynch, & O. B. Williams (Eds.), *Rangelands: A Resource Under Siege* (pp. 404-405). Cambridge: Cambridge University Press.

Dicko-Tour, M. S. (1980). The contribution of browse to cattle fodder in the sedentary system of the Office du Niger. In: H. N. le Houerou (Ed.), *Browse in Africa* (pp. 313-319). International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Dillon, P., & Stakelum, G. (1988). The use of n-alkanes and chromic oxide as markers for determining feed intake, faecal output and digestibility in dairy cows. In: Belclare & Tuam (Eds.), *Proceedings of the 12th General Meeting of the European Grassland Federation, Dublin, Ireland, July 4-7, 1988* (pp. 154-158). Irish Grassland Association, Galway, Republic of Ireland.

D'Mello, J. P. F. (1982). Toxic factors in some tropical legumes. *World Review of Animal Production*, 18, 41-46.

Dos Santos, G. T., & Petit, H. V. (1996). Prediction of total faecal output in sheep fed silage using the Captec chrome controlled-release capsule. *Small Ruminant Research*, 20, 223-227.

Dove, H., Foot, J. Z., & Freer, M. (1989). Estimation of the pasture intake of grazing ewes, using the alkanes of plant cuticular waxes. In: *Proceedings of the XVI International Grassland Congress, 4-11 October 1989, Nice, France* (pp. 1091-1092). Association Francaise pour la Production Fourragere, Versailles, France.

Dove, H., & Mayes, R. W. (1991). The use of plant wax alkanes as a marker substance in studies of the nutrition of herbivores: A review. *Australian Journal of Agricultural Research*, 42: 913-952.

Dove, H., & Mayes, R. W. (1996). Plant wax components: A new approach to estimating intake and diet composition in herbivores. *Journal of Nutrition*, 126: 13-26.

Dove, H., Mayes, R. W., Freer, M., Coombe, J. B., & Foot, J. Z. (1989). Faecal recoveries of the alkanes of plant cuticular waxes in penned and in grazing sheep. In: *Proceedings of the XVI International Grassland Congress, 4-11 October 1989, Nice, France* (pp. 1093-1094). Association Francaise pour la Production Fourragere, Versailles, France.

Doyle, P. T., Casson, T., Cransberg, L., & Rowe, J. B. (1994). Faecal output of grazing sheep measured by total collection or using chromium sesquioxide. *Small Ruminant Research*, 13, 231-236.

Duckworth, J. E., & Shirlaw, D. W. (1955). The development of an apparatus to record the jaw movements of cattle. *The British Journal of Animal Behaviour*, 3: 56-60.

Dulphy, J. P., Remond, B., & Theriez, M. (1980). Ingestive behaviour and related activities in ruminants. In: Y. Ruckebush & P. Thivend (Eds.), *Digestive Physiology and Metabolism in Ruminants* (pp. 103-122). AVI Publishing Company, Connecticut.

El-Aich, A., El-Asraoui, M., & Rittenhouse, L. R. (1991). Effect of trailing to water on temporal behaviour and ingestion of herded sheep in Morocco. *Applied Animal Behaviour* Science, 31: 251-257.

Engel, E. A. N., Van Schalkwyk, A., & Malan, A. (1975). A comparison of three indirect methods for the estimation of feed intake of grazing sheep and cattle. *Agroanimalia*, 7: 23- 26.

Fahey, G. C., & Jung, H. G. (1983). Lignin as a marker in digestion studies: A review. *Journal of Animal Science*, 57: 220-225.

Fahey, G. C., Mclaren, G. A., & Williams, J. E. (1979). Lignin digestibility by lambs fed both low quality and high quality roughages. *Journal of Animal Science*, 48: 941-946.

Fondevila, M., Castrillo, C., Gasa, J., & Guada, J. A. (1995). Rumen-undegradable dry matter and neutral detergent fibre as ration indicators of digestibility in sheep given cereal straw-based diets. *Journal of Agricultural Science, Cambridge*, 125: 145-151.

Forbes, J. M. (1986). *The Voluntary Food Intake of Farm Animals*. (pp 10 -15) Butterworths Ltd, London.

Forbes, J. M. (1988). Metabolic aspects of the regulation of voluntary food intake and appetite. In: *Nutrition Research Reviews* (Vol. 1). (pp 76 -78) Cambridge University Press, Cambridge.

Furnival, E. P., Corbett, J. L., & Inskip, M. W. (1990). Evaluation of controlled release devices for administration of chromium sesquioxide using fistulated grazing sheep 1. Variations in marker concentrations in faeces. *Australian Journal of Agricultural Research*, 41, 969-975.

Furnival, E. P., Ellis, K. J., & Pickering, F. S. (1990). Evaluation of controlled release devices for administration of chromium sesquioxide using fistulated grazing sheep. 2. Variation in rate of release from the device. *Australian Journal of Agricultural Research*, 41: 977-986.

Gaillard, B. D. E., & Richards, G. N. (1975). Presence of soluble lignin-carbohydrate complexes in the bovine rumen. *Carbohydrate Research*, 42: 135-145.

Gallagher, J. R., & McMeniman, N. P. (1988). The nutritional status of pregnant and non-pregnant mares grazing South East Queensland pastures. *Equine Veterinary Journal,* 20: 414-416.

Galyean, M. L., Krysl, L. J., & Estell, R. E. (1986). Marker-based approaches for estimation of faecal output and digestibility in ruminants. In: *Symposium Proceedings: Feed Intake by Beef Cattle* (pp. 96-113). Oklahoma Agricultural Experimental Station, Oklahoma.

Göhl, B. (1981). *Tropical Feeds: Feed Information Summaries and Nutritive Values* (2nd ed.). FAO, Rome.

Goering, H. K., & Van Soest, P. J. (1975). *Forage Fibre Analyses (Apparatus, Reagents, Procedures, and Some Applications) Agriculture Handbook No. 379* (2nd ed), (pp 9 -12) Agricultural Research Service, United States Department of Agriculture, Washington, D.C..

Goldson, J. R. (1963). Observations of the grazing behaviour of grade dairy cattle in a tropical climate. *East African Agriculture and Forestry Journal*, 29: 72-77.

Gränberg, P., & Parkinson, J. R. (Eds.). (1988). *Botswana: Country Study and Norwegian Aid Review.* (pp 35 - 36), Chr. Michelsen Institute, Fantoft.

Greenhalgh, J. F. D. (1982). An introduction to herbage intake measurements. In: J. D. Leaver (Ed.), *Herbage Intake handbook* (1st ed.) (pp. 1-10). The British Grassland Society, Hurley, UK.

Greenwood, G. B., & Demment, M. W. (1988). The effect of fasting on short-term cattle grazing behaviour. *Grass and Forage Science*, 43: 377-386.

Hag, M. G., & Hag, G. A. (1983). Evaluation of acid insoluble ash (AIA) as a marker for predicting the dry matter digestibility of high roughage and high concentrate diets for Sudan desert sheep and goats. *World Review of Animal Production*, 19: 7-10

Haggar, R. J. (1968). Grazing behaviour of Fulani Cattle at Shilka, Nigeria. *Tropical Agriculture*, 45: 178-185.

Haltenorth, T., & Diller, H. (1988). *A Field Guide to the Mammals of Africa Including Madagascar.* (pp 345) Collins, London.

Harker, K. W., Taylor, J. I., & Rollinson, D. H. L. (1956). Studies on the habits of Zebu Cattle. 5. Night paddocking and its effect on the animal. *Journal of Agricultural Science, Cambridge*, 47: 44-49.

Hatfield, P. G., Donart, G. B., Ross, T. T., & Galyean, M. L. (1990). Sheep grazing behaviour as affected by supplementation. *Journal of Range Management*, 43: 387-389.

Hatfield, P. G., Walker, J. W., Fitzgerald, J. A., Glimp, H. A., & Hemenway, K. J. (1993). The effects of different methods of estimating faecal output on plasma cortisol, faecal output, forage intake, and weight change in free-ranging and confined wethers. *Journal of Animal Science*, 71: 618-623.

Hill, D. (1990). *Cattle and Buffalo Meat Production in the Tropics*. (pp 105) ELBS/Longman, London.

Hintz, H. F., Argenzio, R. A., & Schryver, H. F. (1971). Digestion coefficients, blood glucose levels and molar percentage of volatile acids in intestinal fluid of ponies fed varying forage-grain ratios. *Journal of Animal Science*, 33: 992-995.

Hodgson, J. (1982a). Influence of sward characteristics on diet selection and herbage intake by grazing animals. In: J. B. Hacker (Ed.), *Nutritional Limits to Animal Production from Pasture: Proceedings of an International Symposium Held at St. Lucia, Queensland, Australia, August 24 -28, 1981* (pp. 153-186). CAB, Slough, U.K.

Hodgson, J. (1982b). Ingestive behaviour. In: J. D. Leaver (Ed.), *Herbage Intake Handbook* (1st ed.) (pp. 20 –34). British Grassland Society, Hurley.

Hodgson, J. (1986). Grazing behaviour and herbage intake. In: J. Frame (Ed.), *Occasional Symposium: 19. Grazing: Proceedings of a Conference Held at Malvern, Worcestershire 5-7 November 1985* (pp. 51-64). British Grassland Society, Maidenhead, UK.

Hodgson, J. (1990). *Grazing Management: Science into Practice* (1st ed.). (pp 31 - 32), Longman, Harlow, Essex

Hodgson, J., & Rodriguez Capriles, J. M. (1971). The measurement of herbage intake in grazing studies. In: *Annual Report 1970* (pp 132 -141) *Grassland Research Institute*. Hurley.

Hollingsworth, K. J., Adams, D. C., Klopfenstein, T. J., Lamb, J. B., & Villalobos, G. (1995). Supplement and forage effects on faecal output estimates from an intra-ruminal marker device. *Journal of Range Management*, 48: 137-140.

Holst, P. J., Hall, D. G., & Nolan, J. V. (1996). Estimations of pasture and grain intake of prepartum single- and twin-bearing ewes. *Australian Journal of Experimental Agriculture*, 36: 529-532.

Horn, F. P. (1981). Direct measurement of voluntary intake of grazing livestock by telemetry. In: J. W. Wheeler & R. D. Mochrie (Eds.), *Forage Evaluation: Concepts and Techniques* (pp. 367-372). Griffin Press Limited, Armidale, Australia.

Houston, A. I. (1993). The importance of state. In: R. N. Hughes (Ed.), *Diet Selection: an Interdisciplinary Approach to Foraging Behaviour* (pp. 10-31). Blackwell Scientific Publications, London.

Huckle, C. A., Clements, A. J., & Penning, P. D. (1989). A technique to record eating and ruminating behaviour in dairy cows. In: C. J. C. Phillipson (Ed.), *New Techniques in Cattle Production* (pp. 236-237). Butterworths, London.

Humphreys, L. R. (1980). *A guide to better pastures for the tropics and sub-tropics* (4th ed.). (pp 117) Wright Stephenson & Co., Ermington, Australia.

International Livestock Centre for Africa. (1984). *Pastoral Systems Research in Sub-Saharan Africa: Proceedings of IDRC/ILCA Workshop Held at ILCA, Addis Ababa, Ethiopia, March 1983.* (pp 36 -37), ILCA, Addis Ababa.

International Livestock Centre for Africa. (1986). *Modelling of Extensive Livestock Production Systems: Proceedings of the ILCA/ARO/CABO Workshop Held at ARO, Bet Bagan, Israel, 5 - 9 February, 1985* (2nd ed.) (pp 25 - 29). ILCA, Addis Ababa.

Illius, A. W., & Gordon, I. J. (1993). Diet selection in mammalian herbivores: constraints and tactics. In: R. N. Hughes (Ed.), *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour* (pp. 157-181). Blackwell Scientific Publications, London.

Jahnke, H. E. (1982). *Livestock Production Systems and Livestock Development in Tropical Africa.* (pp 24 - 25) Kiler Wissenschaftsverlag Vauk, Postfach.

Janis, C. (1976). The evolutionary strategy of equidae and the origins of rumen and caecal digestion. *Evolution*, 30: 757-774.

Jarvis, A. M., & Cockram, M. S. (1995). Some factors affecting resting behaviour of sheep in slaughterhouse lairage after transport from farms. *Animal Welfare*, 4: 53-60.

Jones, D. I. H. (1981). Chemical composition and nutritive value. In: J. Hodgson, R. D. Baker, A. Davies, A. S. Laidlaw, & J. D. Leaver (Eds.), *Sward Measurement Handbook* (1st ed.), (pp. 243-266). British Grassland Society, Hurley,UK.

Jones, R. J., & Lascano, C. E. (1992). Oesophageal fistulated cattle can give unreliable estimates of the proportion of legume in the diets of resident animals grazing tropical pastures. *Grass and Forage Science*, 47: 128-132.

Judkins, M. B., Krysl, L. J., & Barton, R. K. (1990). Estimating diet digestibility: a comparison of 11 techniques across six different diets fed to rams. *Journal of Animal Science*, 68: 1405-1415.

Kabuga, J. D., Gari-Kwaku, J., & Annor, S. Y. (1992). Pattern and duration of grazing, shade-seeking and drinking behaviour of N'Dama and West African Shorthorn cattle during the day. *Bulletin of Animal Health and Production in Africa*, 40: 167-175.

Keiper, R. R., & Keenan, M. A. (1980). Nocturnal activity patterns of feral ponies. *Journal of Mammalogy*, 61: 116-118.

Kern, D. L., Slyter, L. L., Leffel, E., Weaver, J. M., & Oltjen, R. R. (1974). Ponies versus steers microbial and chemical characteristics of intestinal ingesta. *Journal of Animal Science*, 38: 559-565.

Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals*. (pp 323) Academic Press, London.

Knapka, J. J., Barth, K. M., Brown, D. G., & Cragle, R. G. (1967). Evaluation of polyethylene, chromic oxide and cerium-144 digestibility indicators in Burros. *Journal of Nutrition*, 92: 79-85.

Kotb, A. R., & Luckey, T. D. (1972). Markers in nutrition. *Nutritional Abstracts and Reviews*, 42: 813-845.

Krysl, L. J., Galyean, M. L., Estell, R. E., & Sowell, B. F. (1988). Estimating digestibility and faecal output in lambs using internal and external markers. *Journal of Agricultural Science, Cambridge, 111:* 19-27.

Krysl, L. J., & Hess, B. W. (1993). Influence of supplementation on behaviour of grazing cattle. *Journal of Animal Science, 71*: 2546-2555.

Kurtu, M. Y. (1985). Effect of different grazing time and feed supplementation on the performance of dairy cows in the highlands of Asri region, Ethiopia. *M.Sc. Thesis*, (pp 120) Swedish University of Agricultural Science, Uppsala, Sweden.

Laby, R. H. (1981). Controlled release device for Chromium Oxide. *Australian Patent 555998, issued 1981.*

Laca, E. A., Ungar, E. D., Seligman, N. G., Ramey, M. R., & Demment, M. W. (1992). An integrated methodology for studying short-term grazing behaviour of cattle. *Grass and Forage Science*, 47: 81-90.

Lampkin, G. H., & Quarterman, J. (1958). Observations on the grazing habits of grade and Zebu steers in a high altitude temperate climate. *Journal of Agricultural Science, Cambridge*, 50: 211-218.

Langlands, J. P. (1975). Techniques for estimating nutrient intake and its utilisation by the grazing ruminant. In: C. I. Warner (Ed.), *Digestion and Metabolism in*

the Ruminant (pp 320-332). Arimidale, NSW, Australia: University of New England Publications Unit.

Laredo, M. A., Simpson, G. D., Minson, D. J., & Orpin, C. G. (1991). The potential for using n-alkanes in tropical forages as a marker for the determination of dry matter intake by grazing ruminants. *Journal of Agricultural Science, Cambridge*, 117: 355-361.

Lawrence, P. R., & Pearson, R. A. (1999). *Feeding standards for cattle used for work (*pp 28 - 30). CTVM, Edinburgh.

Le Du, Y. L. P., & Penning, P. D. (1982). Animal based techniques for estimating herbage intake. In: J. D. Leaver (Ed.), *Herbage Intake Handbook* (1st ed.) (pp. 37-75). British Grassland Society, Hurley.

Lippke, H., Ellis, W. C., & Jacobs, B. F. (1986). Recovery of indigestible fibre from faeces of sheep and cattle on forage diets. Journal of Dairy Science, 69: 403-412.

Lowman, R. S., Theodorou, M. K., Dhanoa, M. S., Hyslop, J. J., & Cuddeford, D. (1997). Evaluation of an in-vitro gas production technique for estimating the in-vitro digestibility of equine feeds. In: *Fifteenth Equine Nutrition and Physiology Society Symposium* (pp. 1-2). Fort Worth, Texas: .

Ludlow, M. M., Troughton, J. H., & Jones, R. J. (1976). A technique for determining the proportion of C3 and C4 species in plant samples using stable natural isotopes of carbon. *Journal of Agricultural Science, Cambridge*, 87: 625-632.

Luginbuhl, J. M., Pond, K. R., Burns, J. C., & Fisher, D. S. (1994). Evaluation of the Captec controlled-release chromic oxide capsule for faecal output determination in sheep. *Journal of Animal Science*, 72: 1375-1380.

Lusigi, W. J. (1986). The integrated project on arid lands (IPAL) Kenya. In: P. J. Joss, P. W. Lynch & O. B. Williams (Eds.), *Rangelands: A Resource Under Siege* (pp. 338-349). Cambridge University Press, Cambridge.

Maisels, F. G. (1988). The feeding ecology of the Cyprus *Mouflon ovis* orientalis Gmelin 1774, in the Paphos Forest, Cyprus. (pp 26 -27) *Ph.D. Thesis*, University of Edinburgh.

Malossini, F., Bovolenta, S., Piasentier, E., Piras, C., & Martillotti, F. (1996). Comparison of n-alkanes and chromic oxide methods for estimating herbage intake by grazing dairy cows. *Animal Feed Science and Technology*, 61: 155-165.

Malossini, F., Bovolenta, S., Piasentier, E., & Valentinotti, M. (1994). Variability of n-alkane content in a natural pasture and in faeces of grazing dairy cows. *Animal Feed Science and Technology*, 50: 113-122.

Marais, P. G., Figenschou, D. L., Escott-Watson, P. L., & Webber, L. N. (1996). Administration in suspension-form of n-alkane external markers for dry matter intake and diet selection studies. *Journal of Agricultural Science, Cambridge*, 126: 207-210.

Martin, P., & Bateson, P. (1996). *Measuring Behaviour* (2nd ed.). (135 - 137) Cambridge University Press, Cambridge.

Martin-Rosset, W., Vermorel, M., Doreau, M., Tisserand, J. L., & Andrieu, J. (1994). The French horse feed evaluation systems and recommended allowances for energy and protein. *Livestock Production Science*, 40:37-56.

Matsui, K., & Okubo, T. (1989). A 24-hour automatic recording of grazing and ruminating behaviour in cattle on pasture by a data logger method. *Japanese Journal of Zootechnical Science*, 60: 940-945.

Matsui, K., & Okubo, T. (1990). Automatic recording over a 24-hour period for biting rate during grazing, and chewing rate and number of boluses during rumination of cows on pasture. *Japanese Journal of Zootechnical Science*, 61: 493-500.

Matsui, K., & Okubo, T. (1991a). Automatic recording of heart beat, number of jaw movements and number of pauses in jaw movements every minute for a maximum of 22 days in cattle grazing on pasture. *Animal Science* and *Technology*, 62: 383-389.

Matsui, K., & Okubo, T. (1991b). A method for quantification of jaw movements suitable for use on free-ranging cattle. *Applied Animal Behaviour* Science, 32: 107-116.

Mayes, E., & Duncan, P. (1986). Temporal patterns of feeding behaviour in free-ranging horses. *Behaviour*, 96: 105-129.

Mayes, R. W., Lamb, C. S., & Colgrove, P. M. (1986). The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. *Journal of Agricultural Science, Cambridge*, 107: 161-170.

McCracken, T. A. (1992). The activity and grazing behaviour of horses at pasture. *M.Sc. Thesis*, (pp 36) University of Edinburgh, Scotland.

McDougall, E. I. (1948). Studies on ruminant saliva. 1. The composition and output of sheep saliva. *Biochemistry Journal*, 43: 99-109.

McManus, W. R. (1981). Oesophageal fistulation technique as an aid to diet evaluation of the grazing ruminant. In: J. L. Wheeler & R. D. Mochrie (Eds.), *Forage Evaluation: Concepts and Techniques* (pp. 249-260). CSIRO, East Melbourne.

McMeniman, N. P., Martin, R. G., & Dowsett, K. F. (1990). Intake studies in grazing horses. *Proceedings of the Australian Society of Animal Production*, 18: 112-114.

Meijs, J. A., Walters, R. J. K., & Keen, A. (1982). Sward methods. In: J. D. Leaver (Ed.), *Herbage intake handbook* (1st ed.) (pp. 11-36). The British Grassland Society, Hurley, Maidenhead, Berkshire, UK.

Ministry of Agriculture Food and Fisheries (MAFF). (1987). *MAFF Technical Bulletin: 433. Energy allowances and feeding systems for ruminants.* Ministry of Agriculture Food and Fisheries, London.

Minson, D. J. (1982). Effects of chemical and physical composition of herbage eaten upon intake. In: J. B. Hacker (Ed.), *Nutritional Limits to Animal Production from Pasture: Proceedings of an International Symposium Held at St. Lucia, Queensland, Australia, August 24 -28, 1981* (pp. 167-182). CAB, Slough, U.K..

Mir, P. S., Kalnin, C. M., & Garvey, S. A. (1989). Recovery of faecal chromium used as a digestibility marker in cattle. *Journal of Dairy Science,* 72: 2549-2553.

Moehlman, P. D., Fowler, L. E., & Roe, J. H. (1998). Feral asses (*Equus africanus*) of Volcano Alcedo, Galapagos: behavioural ecology, spatial distribution and social organisation. *Applied Animal Behaviour* Science, 60: 197-210.

Momont, P. A., Pruitt, R. J., Emerick, R. J., & Pritchard, R. H. (1994). Controlled release chromic oxide and alkaline hydrogen peroxide lignin marker methods. *Journal of Range Management*, 47: 418-423.

Mount, L. E. (1979). *Contemporary Biology Series. Adaptation to Thermal Environment.* (pp 396) London: Edward Arnold.

Msiska, J. G. M. (1986). Some anti-nutritional factors in selected tropical legume grains. *M.Sc. Thesis*, CTVM, University of Edinburgh.

Mueller, P. J., Protos, P., Houpt, K. A., & Van Soest, P. J. (1998). Chewing behaviour in the domestic donkey (*Equus asinus*) fed fibrous forage. *Applied Animal Behaviour Science*. 60: 241-253

Mugerwa, J. S., Christensen, D. A., & Ochetim, S. (1973). Grazing behaviour of exotic dairy cattle in Uganda. *East African Agriculture and Forestry Journal*, 39: 1-11.

Muir, J. P., Jordao, C., & Massaete. (1995). Comparative growth characteristics of goats tethered on native pasture and free-ranged on cultivated pasture. *Small Ruminant Research*, 17: 111-116.

Muntifering, R. B. (1982). Evaluation of various lignin assays for determining ruminal digestion of roughages by lambs. *Journal of Animal Science*, 55: 432-438.

Myers, J. S. (1994). The effect of body size, grass height and time of day on the foraging behaviour of horses. *M.Sc. Thesis*, University College of Wales, Aberystwyth.

National Research Council (NRC). (1989). *Nutrient Requirement of Horses*. National Academic Press, Washington, D.C..

Neilson, M. J., & Richards, G. N. (1978). the fate of the soluble lignin-carbohydrate complex produced in the bovine rumen. *Journal of Science Food and Agriculture*, 29: 513-519.

Nelson, D. D., & Tyznik, W. J. (1968). Protein and non-protein nitrogen utilisation in the horse. *Journal of Animal Science*, 32: 68-73.

Nelson, M. L., Motjope, J. W., Finley, J. W., & Parish, S. M. (1990). Ash-free indigestible acid detergent fibre as an internal marker to estimate digestibility with grazing ruminants. *Journal of Range Management*, 43: 224-229.

Nengomasha, E. M. (1997). The donkey (Equus asinus) as a draught animal in smallholder farming areas of the semi-arid regions of Zimbabwe. *Ph.D. Thesis*, (pp 55 -56) University of Edinburgh.

Nichols, G., de la M. (1966). Radio transmissions of sheep's jaw movements. *New Zealand Journal of Agricultural Research,* 9: 468-473.

Njoya, A. (1997). Protein supplementation of grazing cattle in the semi-arid zone of Cameroon. *Tropical Animal Production and Health*, 29: 193-200.

Njwe, R. M., Ikwuegbu, O. A., Tarawali, G., & Little, D. A. (1995). Effects of stocking rate on the botanical composition and nutritive value of diets selected by West African dwarf goats maintained on research-managed and farmer-managed stylo fodder banks during the cropping season in Central Nigeria. *Animal Feed Science and Technology*, 51: 317-328.

Nyamangara, M. E., & Ndlovu, L. R. (1995). Feeding behaviour, feed intake, chemical and botanical composition of the diet of indigenous goats raised on natural vegetation in a semi-arid region of Zimbabwe. *Journal of Agricultural Science, Cambridge*, 124: 455-461.

Ohajuruka, O. A., & Palmquist, D. L. (1991). Evaluation of n-alkanes as digesta markers in dairy cows. *Journal of Animal Science*, 69: 1726-1732.

Parker, W. J., Morris, S. T., Garrick, D. J., Vincent, G. L., & McCutcheon, S. N. (1990). Intra-ruminal chromium controlled release capsules for measuring herbage intake in ruminants: A review. *Proceedings of the New Zealand Society of Animal Production*, 50: 437-442.

Parkins, J. J., Snow, D. H., & Adams, S. (1982). The apparent digestibility of 'complete diet' cubes given to thoroughbred horses and the use of chromic oxide as an inert faecal marker. *British Veterinary Journal*, 138: 350-355.

Payne, W. J. A. (1990). *An Introduction to Animal Production in the Tropics* (4th ed.). Longman, London.

Pearson, R. A., Archibald, R. F., & Muirhead, R. H. (1998). The effect of level of intake on feeding and digestibility of oat straw and alfalfa given to ponies and donkeys. In: *3rd International Colloquium for Working Equines, 5- 9 October 1998* (pp. 286-292). UNAM, Mexico.

Pearson, R. A., & Merritt, J. B. (1991). Intake, digestion and gastrointestinal transit time in resting donkeys and ponies and exercised donkeys given *ad libitum* hay and straw diets. *Equine Veterinary Journal*, 23: 339-343.

Pearson, R. A., & Nengomasha, E. (1994). Improving the productivity of draught animals in sub-Saharan Africa: Existing information relevant to draught animal management studies. In: J. Ellis-Jones (Ed.), *Improving the Productivity of Draught Animals in Sub-Saharan Africa. Report on a Workshop held at Matopos Research Station, Bulawayo, Zimbabwe 17-19 October 1994* (pp. 9-18). University of Zimbabwe, Harare.

Pearson, R. A., & Smith, D. G. (1994). The effect of restricted eating time and work on the dry matter intake and feeding behaviour of cattle and buffalo. *Animal Production*, 58: 339-346.

Penning, P. D. (1983). A technique to record automatically some aspects of grazing and ruminating behaviour in sheep. *Grass and Forage Science*, 38: 89-96.

Penning, P. D., & Hooper, G. E. (1985). An evaluation of the use of short-term weight changes in grazing sheep for estimating herbage intake. *Grass and Forage Science*, 40: 79-84.

Penning, P. D., & Johnson, R. H. (1983a). The use of internal markers to estimate herbage digestibilty and intake. 1. Potentially indigestible cellulose and acid insoluble ash. *Journal of Agricultural Science, Cambridge*, 100: 127-131.

Penning, P. D., & Johnson, R. H. (1983b). The use of internal markers to estimate herbage digestibilty and intake. 2. Indigestible acid detergent fibre. *Journal of Agricultural Science, Cambridge*, 100: 133-138.

Perrier,GK (1986): Activity and forage use patterns of cattle herded by settled Fulani near Zaria, Nigeria. In: *Rangelands: A Resource Under Siege. Proceedings of the 2nd International Rangeland Congress, Adelaide, Australia, 13-18 May 1984.* Australian Academy of Science, Canberra, Australia, 138-139.

Piasentier, E., Bovolenta, S., Malossini, F., & Susmel, P. (1995). Comparison of n-alkane or chromium oxide methods for estimation of herbage intake by sheep. *Small Ruminant Research*, 18: 27-32.

Pinchak, W. E., & Hutcheson, D. P. (1992). Effects of restricted forage intake in confinement on estimated faecal output from a sustained release bolus. *Journal of Range Management*, 45: 129-132.

Preston, T. R., & Leng, R. A. (1987). *Matching Ruminant Production with Available Resources in the Tropics and Sub-tropics* (1st ed.). Penambul Books, Armidale, NSW Australia.

Prior, R. L., Hintz, H. F., Lowe, J. E., & Visek, W. (1974). Urea recycling and metabolism of ponies. *Journal of Animal Science*, 38: 565-571.

Raats, J. G., & Clarke, B. K. (1992). Remote control of oesophageal fistula samples in goats. *Small Ruminant Research*, 7: 245-251.

Raats, J. G., Mogorosi, C. K., Pepe, D., Webber, L. N., Beckerling, A. C., & Tainton, N. M. (1996). Evaluation of the fistula valve technique. 2. Observed feeding behaviour vs. extrusa composition (Poster Presentation). *Bulletin of the Grassland Society of Southern Africa*, 7(Suppl. 1), 66.

Ralston, S. L. (1982). Factors in the control of feed intake of ponies. *Ph.D. Dissertation*, (pp 134 -135) University of Pennsylvania, Philadelphia.

Reeves, M., Fulkerson, W. J., Kellaway, R. C., & Dove, H. (1996). A comparison of three techniques to determine the herbage intake of dairy cows grazing kikuyu (*Pennisetum clandestinum*) pasture. *Australian Journal of Experimental Agriculture*, 36: 23-30.

Reiner, R. J., & Bryant, F. C. (1986). Botanical composition and nutritional quality of alpaca diets in two Andean rangeland communities. *Journal of Range Management*, 39: 424-427.

Rennie, T., Light, D., Rutherford, A., Miller, M., Fisher, I., Pratchett, D., Capper, B., Buck, N., & Trail, J. (1977). Beef cattle productivity under traditional and improved management in Botswana. *Tropical Animal Production and Health*, 9: 1-6.

Romney, D. L., Sendalo, D. S. C., Owen, E., Mtenga, L. A., Penning, P. D., Mayes, R. W., & Hendy, C. R. C. (1996). Effects of tethering management on feed intake and behaviour of Tanzanian goats. *Small Ruminant Research*, 19: 113-120.

Rook, A. J., & Penning, P. D. (1991a). Stochastic models of grazing behaviour in sheep. *Applied Animal Behaviour Science*, 32: 167-177.

Rook, A. J., & Penning, P. D. (1991b). Synchronisation of eating, ruminating and idling activity by grazing sheep. *Applied Animal Behaviour Science*, 32: 157-166.

Rudman, R. (1990). The behaviour and ecology of ferral Burros on St. John, U.S. Virgin Island. *Ph.D. Dissertation*, (pp 234 -235) Cornell University, Ithaca.

Rugh, J. D. (1970). A telemetry system for recording mastication in small animals. *Medical and Biological Engineering*, 8: 497-500.

Rutagwenda, T., Lechner-Doll, M., Schwartz, H. J., Schultka, W., & Engelhardt, W.-von. (1990). Dietary preference and degradability of forage on a semi arid thorn-bush savannah by indigenous ruminants, camels and donkeys. *Animal Feed Science and Technology*, 31: 179-192.

Ruyle, G. B., & Dwyer, D. D. (1985). Feeding stations of sheep as an indicator of diminished forage supply. *Journal of Animal Science*, 61: 349-353.

Schlecht, E., Sangar,, M., & Becker, K. (1995). Feed intake of zebu cattle grazing Sahelian pastures in the dry and rainy seasons. In: K. Becker, P. Lawrence, & B. Orskov (Eds.), *Sustainable Small scale Ruminant Production in Semi Arid and Sub-humid Tropical Areas: Proceedings of an International Workshop, September 1994, at the Institute for Animal Production in the Tropics and Sub-tropics.* (pp. 31-37). University of Hohenhiem, Stuttgart, Germany.

Sein, T., & Todd, J. R. (1988). Investigations into the use of indicator methods of estimating the digestibilities of feeds by ruminant animals. *Journal of Agricultural Science, Cambridge*, 110: 315-320.

Semiadi, G., Barry, T. N., Wilson, P. R., Hodgson, J., & Purchas, R. W. (1993). Growth and venison production from red deer (*Cervus elaphus*) grazing red clover (*Trifolium pratense*) or perennial ryegrass (*Lolium perenne*)/white clover (*Trifolium repens*) pasture. *Journal of Agricultural Science, Cambridge*, 121: 265-271.

Sharma, K., Saini, A. L., Singh, N., & Ogra, J. L. (1998). Seasonal variation in grazing behaviour and forage nutrient utilisation by goats on a semi-arid reconstituted silvipasture. *Small Ruminant Research*, 27: 47-54.

Shenkoru, T. (1987). Nutritive value, dry matter yield and *in vitro* dry matter digestibility as affected by cutting interval and fertiliser application on native natural pasture growing on three soil types at Alemaya University of Agriculture Campus. *M.Sc. Thesis*, (pp 155 - 157) Alemaya University of Agriculture, Ethiopia.

Shrivastava, V. S., & Talapatra, S. K. (1962a). Pasture studies in Uttar Pradesh II. Use of some natural indicators to determine the plane of nutrition of a grazing animal. *Indian Journal of Dairy Science*, 15: 154-160.

Shrivastava, V. S., & Talapatra, S. K. (1962b). Pasture studies in Uttar Pradesh III. Determination of pasture consumption by grazing animal. *Indian Journal of Dairy Science*, 15: 161-166.

Smith, C. A. (1959). Studies on the Northern Rhodesia "Hyparrhenia" veld. 1. The grazing behaviour of indigenous cattle grazed at high and heavy stocking rates. *Journal of Agricultural Science, Cambridge*, 52: 369-378.

Smith, C. A. (1961). Studies in the Northern Rhodesia Hyparrhenia veld. 3. The effect on the growth and grazing behaviour of indigenous cattle of restricting their daily grazing time by night kraaling. *Journal of Agricultural Science, Cambridge*, 56: 243-248.

Smith, T. and Ncube, S. (1995). Sustainable livestock production in an increasingly dry environment. *Farming World,* September 1995.

Spencer, P. (1977). Pastoralists and the ghost of capitalism. In: *East African Pastoralism: Anthropological Perspectives and Development Needs* (pp. 71-92). ILCA, Addis Ababa.

Stevens, C. E., & Hume, I. D. (1995). *Comparative Physiology of the Vertebrate Digestive System* (2nd ed.). (pp 235 - 236) Cambridge University Press, Melbourne, Australia.

Stobbs, T. H. (1973). The effect of plant structure on the intake of tropical pastures I. Variation in the bite size of grazing cattle. *Australian Journal of Agricultural Research*, 24: 809-821.

Stobbs, T. H. (1974). Components of grazing behaviour of dairy cows on some tropical and temperate pastures. *Proceedings of the Australian Society of Animal Production*, 10: 299-302.

Sunvold, G. D., & Cochran, R. C. (1991). Technical note: evaluation of acid detergent lignin, alkaline peroxide lignin, acid insoluble ash, and indigestible

acid detergent fibre as internal markers for prediction of alfalfa, bromegrass, and prairie hay digestibility by beef steers. *Journal of Animal Science*, 69: 4951-4955.

Tamminga, S., Robinson, P. H., Meijs, S., & Boer, H. (1989). Feed components as internal markers in digestion studies with dairy cows. *Animal Feed Science and Technology*, 27: 49-57.

Theodorou, M. K., Williams, B. A., Dhanoa, M. S., McAllan, A. B., & France, J. (1994). A simple gas production method using a pressure transducer to determine the fermentation kinetics of ruminant feeds. *Animal Feed Science and Technology*, 48: 185-197.

Thewis, A., Rodriguez Paz, F., Francois, E., & Bartiaux-Thill, N. (1989). Utilisation of lignin according to Christian as an internal marker for assessing digestibility of temperate grasses with or without supplementation in adult rams. In: *Proceedings of the XVI International Grassland Congress, 4-11 October 1989, Nice, France* (pp. 835-836). Association Francaise pour la Production Fourragere, Versailles, France.

Thorton, C. (1972). *Traveller's Guide to East Africa (Including Ethiopia)* (4th ed.). (pp 28) Thorton Cox, London.

Tilley, J. M. A., & Terry, R. H. (1963). A two stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society*, 18: 104-112.

Trung, L. T., Palo, L. P., Atega, T. A., Bien, R. R., & Lapinid, R. R. (1988). Dose responses of goats fed urea-treated rice straw with varying supplementation rates: Intake and digestibility by markers. In: *Ruminant Feeding Systems Utilising Fibrous Agricultural Residues - 1*987 (pp. 245-251). International Development Program of Australian Universities and Colleges Ltd., Canberra, Australia.

Twerda, M., Fielding, D., & Field, C. (1997). Role and management of donkeys in Samburu and Turkana pastoralist societies in Northern Kenya. *Tropical Animal Production and Health*, 29: 48-54.

Uden,P., Colucci,P. E., & Van Soest, P.J. (1980). Investigation of chromium, cerium and cobalt as markers in digesta rate of passage studies. *Journal of Science Food and Agriculture* 31, 625-632.

Ungar, E. D. (1996). Ingestive behaviour. In: J. Hodgson & A. W. Illius (Eds.), *The Ecology and Management of Grazing Systems* (pp. 185-218). Wallingford, UK: CAB International.

Van Kuelan, J., & Young, B. A. (1977). Evaluation of acid insoluble ash as a natural marker in ruminant digestibility studies. *Journal of Animal Science*, 44: 282-284.

Van Soest, P. J., & Robertson, J. B. (1985). *Analysis of Forages and Fibrous Foods. A Laboratory Manual for Animal Science 613* (pp 124 -128). Cornell University, Ithaca.

Van Soest, P. J., Robertson, J. B., & Lewis, B. A. (1991). Methods for dietary fibre, neutral detergent fibre and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science*, 74: 3583-3597.

Van Soest, P. J., & Wine, R. H. (1968). Determination of lignin and cellulose in ADF with permanganate. *Journal of Official Analytical Chemists*, 51: 780-785.

Vulich, S. A., & Hanrahan, J. P. (1995). Faecal sampling for the estimation of herbage intake using n-alkanes: evaluation of sample pooling and the use of rectal grab samples. *Journal of Agricultural Science, Cambridge*, 124: 79-86.

Vulich, S. A., O'Riordan, E. G., & Hanrahan, J. P. (1991). Use of n-alkanes for the estimation of herbage intake in sheep: Accuracy and precision of the estimates. *Journal of Agricultural Science, Cambridge*, 116: 319-323.

Welch, J. G., & Smith, A. M. (1969). Influence of forage quality on rumination time in sheep. *Journal of Animal Science*, 28: 813-817.

Whittall, H., Mtengeti, E. J., Mtenga, L. A., Romney, D. L., & Owen, E. (1998). Bovine or equine faeces as sources of micro-organisms instead of rumen liquor in the Tilley and Terry *in vitro* digestibility technique for evaluating forages in Tanzania (Poster Presentation) (pp 19), *British Society of Animal Science Annual Meeting, Scarborough 23 -25 March 1998.*

Wilson, P. N. (1961). The grazing behaviour and free-water intake of East African shorthorned zebu heifers at Serere, Uganda. *Journal of Agricultural Science, Cambridge*, 56: 351-364.

Wilson, R. T. (1990). The donkey. In: W. J. A. Payne (Ed.), *An Introduction to Animal Husbandry in the Tropics* (4th ed.) (pp. 581-603). Longman Scientific & Technical, Harlow, Essex.

APPENDIX

Calculation of time spent in a prolonged activity such as foraging

1. Example of Psion organiser output after processing with Word 6 macros to substitute text with behaviour codes:

```
ID  TIME CODE       DATE            TIME            POSITION        ORAL    ATTITUDE
□
B4  C               01/11/1996      11:54:30        1               1       2
B4  C               01/11/1996      12:00:10        1               1       2
B4  C               01/11/1996      12:05:47        1               1       2
B4  C               01/11/1996      12:11:26        1               1       2
B4  C               01/11/1996      12:17:06        1               1       2
B4  C               01/11/1996      12:22:44        1               1       2
B4  C               01/11/1996      12:28:41        1               1       2
B4  C               01/11/1996      12:35:38        1               1       2
B4  C               01/11/1996      12:44:50        1               0       2
B4  C               01/11/1996      12:51:55        1               1       2
```

2. Example of text file imported into Excel 5 Spread sheet.

ANIMAL NUMBER	G1					
TREATMENT	12 HOURS					
COLOUR	GREEN					
ASSIGNED OBSERVATION DAY	TIME CODE	DATE	TIME	POSITION	ORAL	ATTITUDE
1	G	29/10/96	0	0	2	2
3	G	31/10/96	0	0	0	2
3	G	31/10/96	0	0	2	2
2	G	30/10/96	1	0	0	4
3	G	31/10/96	1	0	2	2
3	G	31/10/96	2	0	2	2
3	G	31/10/96	2	0	2	3
2	G	30/10/96	4	0	0	4

3. Example of Excel formulae used to calculate the frequency of each recorded activity

I	J	K	L
	POSITION		
LYING	STANDING	WALKING	OTHER
=IF($E8=0,1,0)	=IF($E8=1,1,0)	=IF($E8=2,1,0)	=IF($E8=5,1,0)
=IF($E9=0,1,0)	=IF($E9=1,1,0)	=IF($E9=2,1,0)	=IF($E9=5,1,0)
=IF($E10=0,1,0)	=IF($E10=1,1,0)	=IF($E10=2,1,0)	=IF($E10=5,1,0)
=IF($E11=0,1,0)	=IF($E11=1,1,0)	=IF($E11=2,1,0)	=IF($E11=5,1,0)
=IF($E12=0,1,0)	=IF($E12=1,1,0)	=IF($E12=2,1,0)	=IF($E12=5,1,0)
=IF($E13=0,1,0)	=IF($E13=1,1,0)	=IF($E13=2,1,0)	=IF($E13=5,1,0)
=IF($E14=0,1,0)	=IF($E14=1,1,0)	=IF($E14=2,1,0)	=IF($E14=5,1,0)
=IF($E15=0,1,0)	=IF($E15=1,1,0)	=IF($E15=2,1,0)	=IF($E15=5,1,0)

4. The observation frequency of each activity in each hour was then calculated.

5. Time spent per hour was then calculated using the equation.

$$AT = \frac{OF}{TO} * 60$$

Where AT is time spent in activity (minutes per hour), OF is observed frequency of activity during one hour and TO is total number of observation in one hour.

Calculation of dry matter intake by double marker, external maker / *in vitro* dry matter digestibility and alkane techniques

A. Example of calculation of faecal output from external marker (C_{36}) concentration in dry faeces

Concentration of external marker in dry faeces	= 116 mg /kg DM
Recovery rate of external marker	= 0.93
Amount of external maker dosed per day	= 308 mg /day
Faecal output per day (from Equation 2.4)	= 308/(116/0.93)
	= 2.86 kg DM / day

B. Example of calculation of digestibility using internal marker (C_{35}) concentration in faeces

Concentration of internal marker in dry faeces	= 248 mg / kg DM
Recovery rate of internal marker	= 0.854
Concentration of internal marker in dry forage	= 113 mg / kg DM
Dry matter digestibility (from Equation 2.5)	= 1- (113/(248/0.854))
	= 0.57

C. Example of calculation of dry matter intake using double marker method (C_{35} and C_{36})

Faecal output per day (from A above)	= 2.86 kg DM / day
Dry matter digestibility (from B above)	= 0.57
Dry matter intake (from Equation 2.3)	= 2.86 / 0.57
	= 5.0 kg DM / day

D. Example of calculation of dry matter intake using dosed even-chain alkane (C_{36}) and natural odd-chain alkane (C_{35})

Amount of C_{36} dosed per day	= 308 mg /day
Concentration of C_{36} in dry faeces	= 116 mg / kg DM
Concentration of C_{35} in dry faeces	= 248 mg / kg DM
Concentration of C_{36} in dry forage	= 2 mg / kg DM
Concentration of C_{35} in dry forage	= 113 mg / kg DM
Dry matter intake (from Equation 2.6)	= (248/116 * 308)/ (113 -(248/116 * 2)
	= 6.1 kg DM / day

E. Example of calculation of dry matter intake using dry faecal output (A) and in vitro dry matter digestibility

Faecal output per day (from A above)	= 2.86 kg DM / day
In vitro dry matter digestibility	= 0.54
Dry matter intake (from Equation 2.3)	= 2.86 / 0.54
	= 5.3 kg DM / day